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Koichi Kaji · Hiroyuki Uno
Hayato Iijima *Editors*

Sika Deer: Life History Plasticity and Management

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Koichi Kaji • Hiroyuki Uno • Hayato Iijima
Editors

Sika Deer: Life History Plasticity and Management

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Editors
Koichi Kaji
Tokyo University of Agriculture and Technology (Retired)
Fuchu, Japan

Hiroyuki Uno
Department of Ecoregion Science
Tokyo University of Agriculture and Technology
Fuchu, Japan

Hayato Iijima
Department of Wildlife Biology
Forestry and Forest Products Research Institute
Tsukuba, Japan

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Cover illustration: A male sika deer at Rusha river in Shiretoko, Hokkaido, northern Japan. (Photo taken on September 3, 2019, by Dr. Hiroyuki Uno)

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Preface

In 2009, the first comprehensive book on sika deer, which aimed to compile and integrate the vast knowledge about sika deer into one source, was published (McCullough et al. 2009, *Sika deer: Biology and Management of Native and Introduced Populations*). As our book is a sequel to this one, we would like to begin by describing how the first sika deer book was published.

We invited Dr. Dale McCullough (currently Professor Emeritus at the University of California, Berkeley) to Japan in 2002. On that occasion, Dr. McCullough visited the deer research fields across the country, found the value of the research accumulated in the region, and proposed the publication of a Sika Deer book on evolution, ecology, behavior, and conservation.

We were overwhelmed by the sheer scale of the project: not only did sika deer move from east to west, north to south, and south to north in response to climate change in the Chinese continent, they also moved in the Japanese archipelago. Deer populations must have aggregated and dispersed in complex ways owing to the establishment and fragmentation of land bridges; this information is highly interesting when considering evolution and adaptation. In contrast to the persistence, stability, and high density of the southern population, the northern population has a winter season, seasonal migration, and an explosive increase, as if they were two different species. The current ecology of sika deer should incorporate this deep historical background to understand its plasticity. This is where insights into genetics and paleontology came into play. Dr. McCullough argued that such an approach would attract a wide readership interested in paleontology, genetics, behavior, biology, and evolution.

As Dr. McCullough predicted, the book has been cited in numerous journals and books in a wide range of disciplines, including mammalogy, ecology, evolution, forest science, genetics, population ecology, conservation ecology, and wildlife management, and has been downloaded in great numbers and continues to attract a large readership.

However, at that time, the knowledgebase was still at a stage where it was not possible to outline the ecological characteristics of the sika deer, especially because of the lack of accumulated research on seasonal migration, morphology, and ecosystem impact. In more than 10 years since the publication of that book, Japan has made great strides in GPS-based behavioral tracking, geographic variation in morphology and evolutionary analysis, genetic analysis, research on population dynamics, and impacts on natural vegetation on a nationwide scale. Overseas (in the United States, New Zealand, and the United Kingdom), research on the hybridization of sika deer with other deer species, interspecies competition, and ecosystem impacts has also advanced. Moreover, the expansion in the distribution and increase in the population of sika deer occurred not only in Japan but also in other countries, and the damage to agriculture and forestry, impact on ecosystems, and impact on other species became a challenge. We are facing conflicting deer issues regarding the conservation of resource values and pest control of sika deer.

Therefore, we decided to compile the new findings from the first publication of the sika deer book and focused on the ecological plasticity of the sika deer, aiming to clarify the ecological characteristics of the deer by integrating studies of different approaches and providing a perspective for management.

This book consists of six parts. Part I introduces the ecological and management background behind the history of sika deer. The next four parts discuss movement ecology (Part II), impact on vegetation and bottom-up effect on sika deer (Part III), impact on ecosystem and its resilience (Part IV), and comparison of life-history characteristics between sika deer and other ungulate species (Part V). The last part (Part VI) covers the science-based management of sika deer.

The authorship of the chapters of this book includes most of the recognized experts and young researchers of sika deer. We hope that the publication of this book will help in the development of the study of sika deer to the next generation.

This book is for professional audiences in the fields of wildlife biology and wildlife management and should be of interest to a wide audience belonging to areas of evolution, genetics, morphology, behavioral ecology, population dynamics, and reproductive physiology.

Fuchu, Japan Koichi Kaji
Fuchu, Japan Hiroyuki Uno
Tsukuba, Japan Hayato Iijima

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First of all, we would like to express our gratitude to all the authors who shared the integrated overall goal of this book and patiently wrote their chapters to complete the book with the latest knowledge and research results. Yoshimi Hayashi carefully went through the entire editing process, including checking for ambiguity in the text, bibliography, and formatting. We could not complete this book without her support. We are deeply grateful to her. Fumiko Yamaguchi, Editor for Biomedical & Life Sciences of Springer Japan, patiently waited for us to realize our plan in publishing and provided us with understanding and continued support. Kavitha Jayakumar, Springer Nature Project Coordinator, also kindly supported all aspects of the editing process. We greatly appreciate both of them. We thank Dr. Yoh Iwasa (former President of the Ecological Society of Japan, Ecological Research Monographs Series Editor) and Dr. Atsushi Kume (Director of Publications, Ecological Society of Japan) for suggesting this book to be published as a part of the Ecological Research Monographs Series and for patiently waiting for the opportunity to do so. Finally, we would like to express our deepest gratitude to Dr. Dale McCullough for his profound understanding and efforts to establish science-based wildlife management in Japan and convey his warm message that he heartily endorses the last sentence about future generations in the Preface. We sincerely thank all and hope that the outcome of this book will be a response to their contributions.

Koichi Kaji, Hiroyuki Uno, Hayato Iijima

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Chapter 1
Introduction

Koichi Kaji, Hiroyuki Uno, and Hayato Iijima

Abstract The sika deer (*Cervus nippon*) has been of great economic and scientific interest; however, it has problems such as hybridization with related species, impact on other species, damage to agriculture and forestry, and impact on ecosystems worldwide. The history of the relationship between deer and humans has changed from hunting targets to religious objects, protected animals, and pests, owing to changes in the socioeconomic and natural environment in Japan. Sika deer expanded their range and increased their numbers in recent decades, and the management goal for the sika deer for the last 25 years has been to reduce the overabundant population and damage on agriculture, forestry, and natural environment. The coexistence of deer and humans in a shrinking society with fewer hunters has become a major social issue. This volume presented the ecological and management background behind the history of sika deer and the outline of a chapter of this book as an introduction.

In 2009, the first comprehensive book on sika deer was published (McCullough et al. 2009, *Sika Deer: Biology and Management of Native and Introduced Populations*) to integrate knowledge about the biology and management of native and introduced sika deer globally. The book successfully explored their basic biology, behavior, and ecology, including their management and conservation and recovery of threatened populations. It continued to attract many readers. In the introduction of the book, McCullough (2009) posed the following question: why could no other deer match the sika in its ability to strip the vegetation bare and expose soils to massive erosion, thereby creating a wasteland? Another critical question asked is how sika deer could

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K. Kaji (✉)
Tokyo University of Agriculture and Technology (Retired), Fuchu, Japan
e-mail: kkaji@cc.tuat.ac.jp

H. Uno
Faculty of Agriculture, Tokyo University of Agriculture and Technology, Fuchu, Japan
e-mail: unoh@go.tuat.ac.jp

H. Iijima
Department of Wildlife Biology, Forestry and Forest Products Research Institute, Tsukuba, Japan
e-mail: hayato.iijima@gmail.com

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maintain high densities in degraded habitats for long periods. Some ungulate populations are highly abundant in temperate forests under long-term heavily browsed habitats (Simard et al. 2008; Saout et al. 2014). However, there are limited studies on the processes and mechanisms that allow ungulate populations to maintain high abundance despite the dramatic decline in food plants (Simard et al. 2008; Ueno et al. 2018).

The current book tries to answer why sika deer significantly impact the environment, compared to other deer species, and forecasts key ecological characteristics of sika deer "plasticity." Since the first book was published in 2009, research on ecology, population dynamics, and movement ecology using GPS collars, as well as on geographical variation of morphology, as ecological and evolutionary responses in sika deer, has advanced during the last decade. The new sika book has been updated with current knowledge on sika deer distribution, ecology, and management, focusing on their high ecological plasticity and discussing future challenges for their management and research.

To begin, we described the history of sika deer in relation to their ecological characteristics and management background because the current ecology of the sika deer should reflect this deep historical background, which has led to their plasticity.

1.1 Ecology and Management History of Sika Deer in the Japanese Archipelago

1.1.1 Ecological Characteristics of Sika Deer

In the early Pleistocene, sika deer inhabited only northern China and Taiwan, but from the Middle Pleistocene to the Holocene, they expanded to northeastern, central, southwestern, and southern China; east of Mongolia-Xinjiang region; Qinghai-Tibet region; northern Vietnam; Siberia; Korea; and Japan (Jiang et al. 2016). Sika deer are currently distributed in northeastern Asia, from Vietnam in the south, through China and Korea to the Ussuri area (Russian) in the north, and on the continental islands of Taiwan and the Japanese archipelago (Ohtaishi 1986; Whitehead 1993; McCullough 2009). Sika deer prefer climates warmer than those preferred by red deer and are distributed between 15° N and 45° N, while the southernmost distribution of red deer is located at approximately 26° N. Sika deer are only found at much higher elevations in the foothills of the Himalayas (Geist 1998). Since the early 1990s, sika deer in Asian habitats have been decimated by overhunting and habitat loss in many areas. They have been restricted to forest patches in the mountainous regions of East Asia; however, natural populations in Far Eastern Russia and reintroduced populations in Taiwan are recovering their distribution (Ohtaishi 1986; Aramilev 2009; McCullough 2009).

Sika deer are classified into 14 subspecies based on body size, antler size, and pelage color, of which four subspecies (three in China and one in Taiwan) were extinct in the wild. However, some subspecies were domesticated and kept in deer farms in China; six subspecies inhabited the Japanese archipelago (Ohtaishi 1986). Sika deer have been widely introduced in Europe, New Zealand, and the USA, among other places (Whitehead 1993; Dolman and Wäber 2008).

"Sika" means deer in Japan, while the sika deer is called "mei hua lu" in China and "hua lu" in Taiwan, words which mean "(plum) blossom deer": the elegant pattern of white spots against a rusty red background in the summer coat looks similar to a "plum blossom." The white-spotted pattern is considered to be a protective color to protect against predators, mimicking sunlight filtering through the trees in summer. The white spot disappears in the dark brown winter coat, which is similar to that of dead leaves and dead trees, making it difficult to distinguish. Where sika have been introduced to Europe and New Zealand, hybridization with red deer and wapiti has been a major concern (Chaps. 29 and 31). In Far East Russia, the natural ranges of sika and wapiti have been noted to overlap; moreover, hybridization occurs, but it is fairly rare (Heptner et al. 1989; Aramilev 2009).

Most of the continental sika deer are of the same size as Honshu sika; however, body size in the sika deer in the Japanese archipelago has a large geographical variation. The winter body mass of adult males (around 6 years old) is 120 kg for northern Hokkaido sika, compared to 35 kg for Yaku sika and 30 kg for Kerama Sika in the southern islands, indicating a fourfold difference (Ohtaishi 1986). Hokkaido sika grows fast and has large antlers and many branches (four or five on each side), while the southern island deer grow slower and have a smaller antler with fewer branches (three on each side) (Ohtaishi 1986). These geographical differences in antler size and branches are evidenced in "island dwarf" individuals with a tendency toward reduced antlers, "primitive" antlers, short legs, and small bodies on the island, where there have been no culling predators (Geist 1998).

The body size of Honshu sika excavated from the mainland, which lived there during the early Jomon period (6000 BC–5000 BC), is comparable to that of present-day Hokkaido sika; however, the body size became smaller in the late Jomon period (3000 BC–2300 BC) (Ohtaishi 1986; Koike and Ohtaishi 1985, 1987). Currently, there exists a clear latitudinal cline of body size (body mass and skull size) for sika deer-associated climatic conditions, which is consistent with Bergmann's rule (Chap. 6). In addition to Bergmann's rule and island rule, local adaptation of limb length was found in the sika deer population living in rugged terrain in southern Japanese islands. The relative limb length of sika deer populations in southern Japanese islands is shorter on islands with steep slopes (Terada et al. 2012). Genetic studies have demonstrated that the difference in relative limb length between the two of eight populations was consistent with local adaptation hypothesis, although conclusive results were not obtained for the other populations (Terada and Saitoh 2018). As an ecological and evolutionary response, sika deer showed high phenotypic plasticity of morphology related to climatic conditions and local adaptation.

Recent studies involving sika deer mitochondrial DNA analysis indicated a genetically distinct north and southern type at the border between the Kinki and Chubu regions of Honshu in Japan (Tamate 2009). There are two hypotheses to explain these differences with either separate colonization events via land bridges from mainland Asia (multiple-colonization hypothesis) or isolation of the descendants of a single invasion in different Pleistocene glacial refugia (refugia hypothesis) (Tamate et al. 1998; Nagata et al. 1998; Goodman et al. 2001). During the last glacial period, the Late Pleistocene (15,000 to 10,000 years ago), most of the Honshu was dominated by boreal coniferous and mixed coniferous forests, with broadleaf forests remaining only in very limited areas. The refuge hypothesis suggests that different lineages of large mammals, such as the Japanese macaque (*Macaca fusciata*) and Japanese black bear (*Ursus thibetanus*), survived in broad-leaved forests as refuges and expanded their distribution with the expansion of temperate forests after the last glacial period (Tamate 2009).

It was estimated that the colonization and separation of the sika deer occurred in the Japanese islands less than 0.5 million years ago before the present (Nagata et al. 1998). Archaeological evidence indicates that humans first appeared in the Japanese archipelago during the Late Pleistocene, 40,000 to 30,000 years ago. Sika deer were a major player in the forest ecosystem before humans colonized Japan, but during the last glacial period, most of the forests in the Japanese archipelago were covered with coniferous trees; thus, the sika deer are considered to have small populations due to limited suitable habitats.

1.1.2 History of Interaction between Sika Deer and Humans in the Japanese Archipelago

During the Jomon period, sika deer and wild boar were the main game species in Japan. During the Yayoi period (1000 BC–300 AD), when rice cultivation began, the role of hunting declined because of the use of domestic animals such as pigs, and sika deer became an object of worship. The beginning of agriculture in the Yayoi period was also the beginning of the struggle against wildlife damage. Sika deer were depicted on bronze bell-shaped vessels and earthenware, and many deer clay figurines were excavated during the Kofun period (mid-third century to mid-seventh century). This is because the life force of deer antlers, which fall off in spring and regenerate, is compared to the growth of rice. Since the eighth century, deer in Nara Park, which have been known as "shinroku," are considered messengers of the gods in the Shinto religion and have been protected by shrines since the thirteenth century, creating a unique cultural and biological relationship between humans and deer (Torii and Tatsuzawa 2009).

Originally, sika deer were widely distributed from Hokkaido to Kyushu in Japan. There was no significant change in the distribution area of deer for approximately 10,000 years from the Jomon period to the early eighteenth century, but from the late eighteenth century to the mid-twentieth century, habitat destruction and overhunting caused a significant reduction in the distribution of sika deer on Honshu island (Tsujino et al. 2010). The distribution of Hokkaido sika populations has also been reduced due to overexploitation during the same period (Kaji et al. 2000; Uno et al. 2009).

For the Ainu and the Japanese, the wolf was a god and an object of worship. Wolves in Hokkaido were exterminated via subsidies and by using poisons by 1890. As the number of deer decreased due to overhunting and mass deaths from heavy snowfall, they began to attack livestock. Wolves in Honshu were also exterminated in the early 1900s due to increased damage to horses and humans suffering from rabies (Knight 2003; Walker 2005).

By 1600, Japan had more of the world's most powerful guns than any other country. However, guns were not abandoned even after the end of the era of warfare in the sixteenth century, and throughout the seventeenth century, guns became popular in farming and mountain villages as agricultural tools and greatly contributed to labor-saving in pest animal control (Tsukamoto 1983).

Yoshino foresters have been continuing the traditional forestry work of their fathers for 400 years in Nara Prefecture, central Japan. *The Yoshino Forestry Complete Book*, a forestry technical book published in 1898, states that there is no place where wildlife damage is not present, i.e., it is everywhere, and that it is essential for forestry to take measures against wildlife damage. Agriculture and forestry in the Edo period could not have existed without any measures to control deer. However, in the sixteenth and seventeenth centuries, tens to hundreds of thousands of deer skins used for armor were imported annually from Southeast Asia.

From the end of the Edo era to the middle of the Meiji era (spanning approximately from 1850 to the 1880s), Japan's forests were at their most desolate, with many "bald mountains" and degraded forest areas in low mountain ranges throughout the country and frequent landslide disasters (Ohta 2012). People overused forests for building materials, fuel, fertilizer (for rice cultivation), fodder (for livestock), and widespread slash-and-burn agriculture. After the turmoil of the Meiji era (1868–1912), deforestation began in the mid- to high-elevation areas of remote mountains. After World War II, the large area of deforestation in remote mountain areas changed dramatically.

With the fuel revolution in the mid-1960s, fuel dependence on wood and charcoal forests was replaced by oil. People withdrew from the mountains to plant coniferous trees on a large scale, known as expanded afforestation (Yamaura et al. 2012). In this way, Japan regained its "rich greenery" for the first time in 400 years, as artificial forests planted in the past 40 to 50 years have grown out of the forest devastation that had continued for more than 300 years (Ohta 2012). In addition, rice paddies were turned into fields as human population decreased, and pastures were created up to high altitudes. These changes in the landscape created enormous feeding grounds for deer.

Since the mid-1990s, the decline in farming activities due to the declining and aging population in rural areas has led to an increase in abandoned farmland and pastureland, which in turn has led to an increase in the number of deer, more damage, and an increase in abandoned farmland that has been termed "a chain reaction of negativity" (Chap. 2). As a result, the distribution area of sika deer increased 2.7 times from 1978 to 2018, covering 70% of the national land area (Chap. 2). The number of deer captured has increased 14-fold in 30 years, from 42,000 in 1990 to 602,900 in 2019. However, the distribution continues to expand in the Tohoku region, which was a blank area of deer distribution in the mid-twentieth century (Chap. 2). The overabundance of deer has not only caused damage to agriculture and forestry but has also affected natural vegetation, soil erosion, seed banks, local fauna, and ecological communities.

The management goal of sika deer for the last 25 years has been to reduce the overabundant population and reduce damage to agriculture, forestry, and natural environment. As described above, the relationship between deer and humans has changed from hunting targets to religious objects, protected animals, and pests, owing to the change in socioeconomic and natural environment. The coexistence of deer and humans in a shrinking society with fewer hunters has become a major social issue.

1.2 Chapter Outlines of the Book

To address the upcoming issue of sika deer management in a shrinking society, the ecological characteristics of sika deer should be clarified. This book will present current knowledge about the ecological characteristics of sika deer, particularly focusing on their singular plasticity, as well as how their population maintains high densities and has a large impact on local ecosystem. We believe that this is the most comprehensive book on the ecology and management of sika deer. It is organized into six parts. Part I introduces the ecological and management background behind the history of sika deer. The next four parts discuss movement ecology (Part II), impact on vegetation and bottom-up effect on sika deer (Part III), impact on the ecosystem and its resilience (Part IV), and comparison of life-history characteristics between sika deer and other ungulate species (Part V). The last part (Part VI) covers the science-based management of sika deer.

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This book is for professional audiences in the fields of wildlife biology and wildlife management and should be of interest to a wide audience belonging to areas of evolution, genetics, morphology, behavioral ecology, population dynamics, and reproductive physiology.

- Expansion of deer distribution on a national scale and its impact on vegetation: past, present, and future (Chaps. 2 and 3).
- Harvest-based model for population estimation, characteristics of population dynamics, and variation in local deer density (Chaps. 4 and 5).
- Variation in morphology associated with local adaptations to habitat and variation in reproduction related to population density (Chaps. 6 and 7).

- Factors affecting movement patterns and behavior of sika deer (Chaps. 8, 9, 10, 11, 12, 13 and 14) and sika deer in clear-cut areas (Chap. 15).
- Plasticity in food habits and impact on vegetation and seed banks (Chaps. 16, 17, 18, 19, 24, 25 and 26).
- Protection of vulnerable plants and seeds (Chaps. 20 and 26).
- Impact on soil properties and erosion (Chaps. 23, 24 and 27).
- Impact on ecological community and its resilience (Chaps. 21, 22 and 27).
- Interspecific competition between sika deer and other ungulate species (Chaps. 28, 29, 30 and 31).
- Science-based management: adaptive management, zone-based management, and unit-based management (Chaps. 32, 33, 34 and 35).
- Future challenges for research and management of sika deer (Chap. 36).

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Part I

History, Distribution and General Characteristics

Chapter 2
The Process of Population Expansion of Sika Deer

Teruki Oka, Hayato Iijima, Atsushi Kamata, Akira Ishida, Norikazu Eguchi, Takuya Aikawa, Hiroshi Takahashi, Hiroshi Kondoh, Chizuru Yayota, Masato Hayakawa, and Toru Koizumi

Abstract The battle between the Japanese people and sika deer has been going on for a long time. Due to the postwar policy of protecting female deer and their phenomenal reproductive ability, the distribution of sika deer is expanding rapidly, covering 70% of the country as of 2018. The speed of distribution expansion itself

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T. Oka (✉)
Shikoku Research Center, Forestry and Forest Products Research Institute, Kochi, Japan
e-mail: okat@affrc.go.jp

H. Iijima
Department of Wildlife Biology, Forestry and Forest Products Research Institute, Tsukuba, Japan
e-mail: hayatoi@affrc.go.jp

A. Kamata · A. Ishida
Aichi Forestry Research Institute, Shinshiro, Japan
e-mail: atsushi_kamata@pref.aichi.lg.jp; akira_ishida@pref.aichi.lg.jp

N. Eguchi
Department of Environmental Science, University of Human Environments, Okazaki, Japan
e-mail: n-eguchi@uhe.ac.jp

T. Aikawa · H. Takahashi
Tohoku Research Center, Forestry and Forest Products Research Institute, Morioka, Japan
e-mail: taikawa@affrc.go.jp; tkhshrs@affrc.go.jp

H. Kondoh
Kyushu Research Center, Forestry and Forest Products Research Institute, Kumamoto, Japan
e-mail: kondoh@affrc.go.jp

C. Yayota
Kansai Research Center, Forestry and Forest Products Research Institute, Kyoto, Japan
e-mail: yayota@affrc.go.jp

M. Hayakawa
MapQuest Corporation, Toyohashi, Japan
e-mail: hayakawa@mapquest.co.jp

T. Koizumi
Tama Forest Science Garden, Forestry and Forest Products Research Institute, Hachioji, Japan
e-mail: koizmy@affrc.go.jp

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and the speed of agricultural and forestry damage caused by expansion seem to be constant. Citizen science is highly important to adapt to the expanding distribution of sika deer and to reduce its damage, sharing information on deer among government officials, local residents, forestry and agricultural workers, members of hunting associations, hikers, nature lovers, and sometimes researchers and finding solutions based on this information.

2.1 History of the Relationship Between Sika Deer and People in Japan

The Ministry of the Environment (MOE 2021) conducted the deer distribution surveys as a part of the National Survey on the Natural Environment, denoted by filling a regional grid [one grid square is equivalent to approximately 5 km by 5 km (Fig. 2.1)]. In recent years, the distribution of sika deer in Japan has expanded remarkably. In 1978, these deer were distributed across approximately 25% of Japan's total land area. In 2018, the area of distribution of the deer exceeded 11,000 grid squares, which was approximately 2.7 times greater than the case in 1978, and accounted for approximately 70% of Japan's total land area. As males were found in the northern part of Ibaraki Prefecture in 2017, there were no

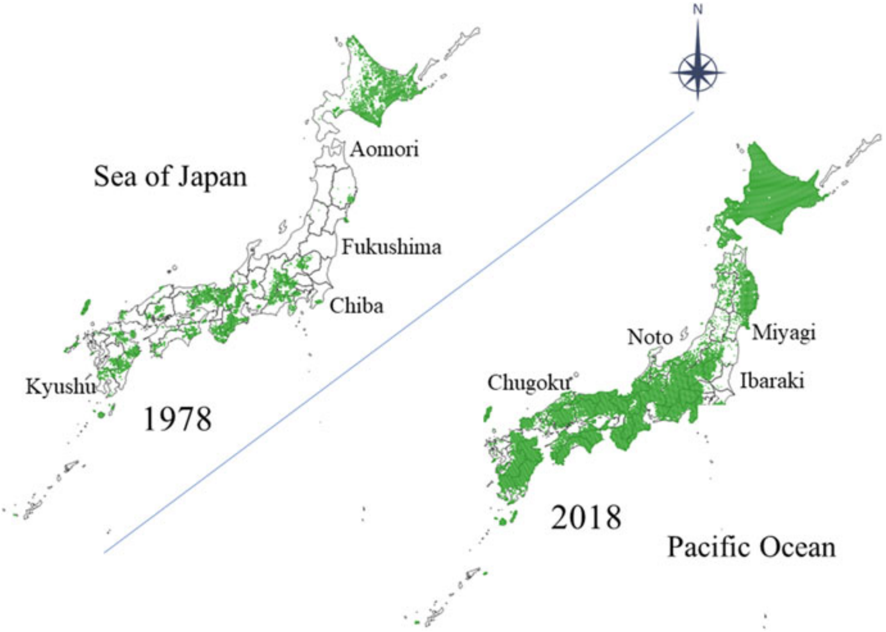

Fig. 2.1 Sika deer distribution in Japan in 1978 and 2018. (Source: Ministry of the Environment (2021))

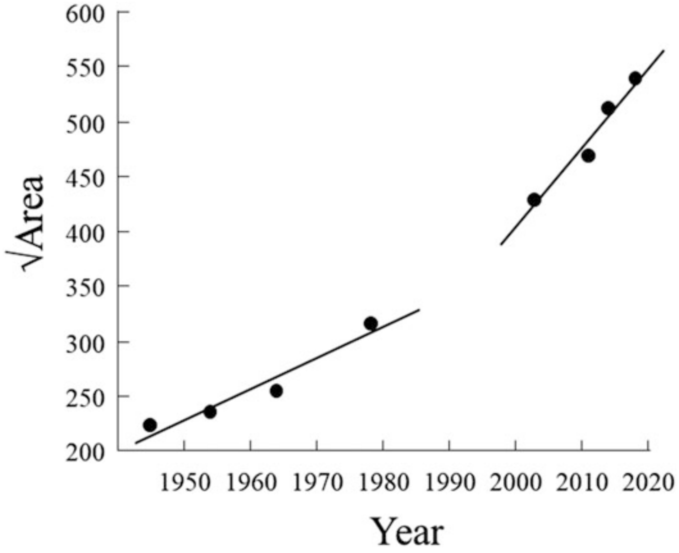

Fig. 2.2 Expansion of the square root of the total distribution area of sika deer from 1945 to 2018. 1945–1978: $y = 2.826x - 5283.2$, $R^2 = 0.9395$. 2004–2018: $y = 7.403x - 14405.0$, $R^2 = 0.9583$. [Source: Ministry of the Environment 2021 (1978, 2004, 2011, 2014, and 2018), Koizumi et al. 2018 (1945, 1954, and 1964)]

prefectures in which deer were not found, and the only relatively large areas of nondistribution remaining were from Aomori to the Noto Peninsula along the Sea of Japan, from the south of Miyagi through Fukushima to the northern part of Chiba, parts of the Chugoku and Kyushu region, and the metropolitan area. A trend graph of the square root of the total area of distribution from 1945 to 2018 shows a positive slope (Fig. 2.2). The slope of the graph is said to correspond to the rate of distribution expansion by a mathematical model that combines random diffusion and logistic growth in a two-dimensional space. The rate at which a newly introduced animal expands its distribution in a given region through repeated reproduction and migration is known to be determined by the diffusion coefficient D and the population growth rate r of a given animal in a given region (e.g., Skellam 1951; Elton 1958; Okubo et al. 1989; Andow et al. 1990).

There are some hypotheses to explain the expansion of the deer distribution. Perhaps climate change has increased the average temperature, and there has been a lower rate of occurrence of heavy snowfall and abnormally low temperatures in winter than before, reducing winter mortality rates, particularly of fawns (Ueno et al. 2018). Secondly, human pressure on wildlife has been weakened; this is considered to be the most important reason.

Although this chapter discusses the expansion of deer distribution, it is a fact that the deer distribution is recovering in the historical ranges, not expanding into the new area. From the presence of remains of sika deer excavated from archaeological sites of the Jomon (14,000 BC–1000 BC) ruins, Tsujino et al. (2010) showed that sika deer were once widely distributed everywhere in the Japanese archipelago and the surrounding islands. The Jomon people depended on the products of hunting and gathering for food and other necessities of life. As time went on, in the Yayoi period (1000 BC–300 AD), people began to depend on agriculture for their livelihood and developed a settled agricultural society. Crop damage caused by deer must have begun with the beginning of agricultural culture. It is thought, based on artifacts excavated from shell mounds and other sources, that hunting and fishing had also continued since the Jomon period, but sika deer may have been hunted near the paddy fields to prevent crop damage (Takahashi 2009).

The meat-eating ban issued by Emperor Temmu in 675 is often taken up when discussing the history of meat-eating in Japanese society (e.g., Krämer 2008), and its significance is often debated (Nakazawa 2018). Interestingly, the meat that was banned in this decree did not include sika deer meat, which is thought to have been eaten at that time. These deer may have already been regarded as vermin in this era, and the decree may reflect both the importance of sika deer as a protein source for people and the threat they posed to rice cultivation. This trend continued down through the ages. According to many ancient documents and folklore materials from the 1600s and 1700s, fences, stone walls, and earthworks built between mountains and agricultural land that are called *shishi-gaki* are remnants of defenses against deer and wild boar, which are harmful to agriculture and forestry (Takahashi 2010). Moreover, in the 1600s and 1700s, deer were handled not only by erecting fences and driving the animals away but also by putting strong pressure on people to hunt them, with hunters being employed as "pest controllers" by the agricultural estates (Takei 2010). Furthermore, it appears that the lords of the domain and the local authorities mobilized many laborers and hunted tens of thousands of deer over a very short time. With the development of new fields, vast areas of land were developed, reclaimed, and converted to farmland; the extermination of these deer was actively carried out at a scale very much larger than that of the current capture system. At present, efforts to prevent damage by deer as much as possible involve erecting deer fences on farmland and forest land and repelling and capturing deer; however, these measures are not new. Since the dawn of history, there has been a running battle between Japanese people and sika deer.

Around 1900, deer became an object of sport hunting, and a pelts animal market was formed. They were traded as a war material, and the commercial capture of deer grew. Overexploitation was widespread, deer populations shrank in various parts of Japan, and their habitats became fragmented. When the postwar chaos had subsided, the deer lived in very few places, and they were seen rarely. When the Hunting Law was revised to the Wildlife Protection and Hunting Act (1963), it was quite natural to include the idea that deer were animals to be protected. When sika deer had to be protected, female deer that could give birth to fawns were excluded from the targets of hunts.

In retrospect, and considering the current situation of increasing damage caused by deer, this was likely one of the factors contributing to the expansion of their distribution and may represent a turning point in deer management in Japan. Female deer are very fertile and give birth to offspring year after year (e.g., Suzuki and

Ohtaishi 1933; Koizumi et al. 2009). It was way that researchers found that the annual rate of increase was 20% (Kaji et al. 2004), with 1000 deer reaching 15,000 in 15 years.

In addition, social factors have helped change the balance between people and deer. Since the World War II, urbanization has advanced, leading to the depopulation of much of the countryside. Some rural communities may die out entirely as the younger generations migrate to the cities, leaving behind populations that are disproportionately elderly. Despite passing the Law on Special Measures for Activation of Depopulated Area (depopulation law) in 1970 to restrain the population decline by providing government resources for depopulated areas, the government could not halt the tide of out-migration. There is now less activity in villages than in the past, and many villages have become largely silent. Abandoned farmland and abandoned orchards have become suitable habitats to attract deer by providing both shelter and sources of high-energy foods, which accelerates the rate of reproduction of the deer and the growth of deer populations. The damage to those lands increases further, which reduces the motivation of the farmers to produce and promotes depopulation, resulting in even more abandoned farmland and "a chain reaction of negativity." Indeed, the rate of expansion of the deer distribution seems to have accelerated between 1978 and 2004 (Fig. 2.2).

Eventually, the balance between deer reproduction and human pressure was almost lost. The capture of deer by people failed to catch up with the increase of deer. To reduce the deer numbers, it became necessary to catch female deer. The prefectures of Hokkaido, Iwate, and Hyogo decided to allow the hunting of female deer in 1994, and the number of prefectures that followed suit gradually increased. However, the ban on female deer hunting was not lifted nationwide until 2007. In fact, deer have been protected for approximately 60 years, during which time their distribution has recovered.

Sika deer have now become the worst offenders in respect of harm to agriculture and forestry. According to the Ministry of Agriculture, Forestry, and Fisheries (MAFF), the damage to agricultural products caused by deer amounted to approximately 5.4 billion yen/year, accounting for approximately 34% of the total caused by wild birds and animals, and deer damaged approximately 4200 hectares of forestry, accounting for approximately 72% of the total. The estimated amount of deer damage to agriculture and forestry as a whole could reach approximately 10 billion yen. Moreover, it has been pointed out that the strong appetite of deer destroys the ecosystem by feeding the understory vegetation and endangering rare plant species (e.g., Tamura 2019). It has also been pointed out that there are risks associated with national land conservation, such as erosion or landslides on slopes that have lost support from plants (Wakahara et al. 2008).

In 2013, MOE and MAFF developed the "Drastic Measures to Strengthen the Capture of Birds and Animals," with the aim of halving the deer population by 2023. In 2015, the Protection and Control of Wild Birds and Mammals and Hunting Management Law (Wildlife Protection Law) was amended to designate sika deer as Type II Specified Wildlife, establish a business to capture wild birds and animals under designated management, introduce a certified wild animal culling business operator system, grant permission for anesthesia shooting in residential areas, and reduce the age for obtaining a net hunting license and a trap hunting license, with the aim of promoting deer capture and fostering hunt operators. Although the management of wild animals that harm agriculture and forestry depends on a balance between economic standards of acceptable damage and conservation standards of acceptable capture, conservation standards are of little concern when dealing with the current deer problem.

2.2 Deer Expansion in Front of the Distribution Edge: Example in the Northern Tohoku Region

By 2014, the areas of deer distribution in Aomori and Akita prefectures in the northern part of Honshu Island were still small. Although the fear of deer invasion was strong for these prefectures, no measures can effectively manage deer without their information. Local governments started to compile and plot data on deer sightings on printed maps in respect of locations. When a deer invades land that it has not been confirmed as inhabiting either previously or for some time, the first information obtained is usually from people who say something such as “I saw a deer,” “A deer was hit by a vehicle,” or “A deer caught in a trap” (hereinafter referred to as eyewitness information). Moreover, in the season when males have antlers, gender information can be added.

Arranging these data to be input on GIS (geographic information system) will be more effective for developing measures to be taken in the future. Visualizing the pattern of such eyewitness information and arranging such data in chronological order, one can see the process from the past to the present. The following is an overview of the frontline of the distribution of sika deer in the Tohoku region, as revealed by the accumulation of these eyewitness information.

Mt. Goyo, located in the southeastern part of Iwate Prefecture near the southern end of the Kitakami Mountain range, supplied the Sendai Date clan with cypress, an important forest resource. As the Date clan was armed with guns, entering or using the mountain resources was strictly restricted as they were under the direct control of the clan. Deer were also a useful resource in the region, as meat, fur, and antlers were offered as annual tribute. Subsequently, the deer population declined because of overhunting in the first half of the twentieth century; however, it then recovered, thanks to conservation policies. As shown in the results of the National Survey on the Natural Environment, in 1978 deer were found only on Mt. Goyo and Oshika Peninsula, Miyagi, in the Tohoku region in 1978 (Fig. 2.1). In the second half of the 1980s, damage to agricultural products became a problem around Mt. Goyo, and Iwate Prefecture established a countermeasure committee in 1990 to manage the area’s deer population scientifically. This included the permission to hunt female deer that was granted in 1994. In 2000, the first deer conservation and management plan (Phase 1: 2000–2002) focusing on the Mt. Goyo area and its surroundings was

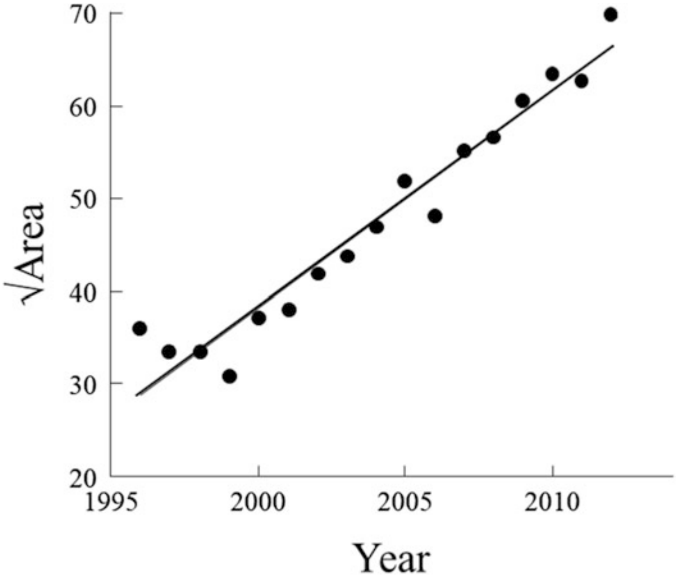

Fig. 2.3 Expansion of the square root of the total culled area from 1996 to 2012 in Iwate. $y = 2.335x - 4632$, $R^2 = 0.9426$. (Source: Iwate Prefecture)

formulated, being zoned into four areas, each of which was assigned a different level of severity in terms of measures against deer (e.g., Iwate Prefectural Government 2017).

The plan divides the main area of Mt. Goyo into three zones starting from the center. These are a protected area, a controlled hunting area, and a population control area. Based on the amount of *Sasa* spp., which is the main food for deer in winter, the estimated carrying capacity in the three zones is calculated as being 2000 animals. The fourth zone, which is located outside of the main area of Mt. Goyo, is designated as a restricted area, and deer have been actively captured to suppress expansion of this habitat. Based on the number of deer counted in the 2000 aerial survey and the estimated reproduction/death rate, the number in each following year has been calculated by statistical processing, compared to the estimated carrying capacity.

Counting the number of animals is difficult. Even though the methods considered the most scientific at the time were used, they were not in harmony with the reality of the situation, and discussions continued at the review committee. While the committee is discussing the population of Mt. Goyo and the surrounding area, carrying out the conservation and management plan Phase 1 and 2 (2002–2007), the range of the deer expanded gradually northward. Small populations in the restricted area were left to local efforts without finding effective means of capture. The damage to agricultural products was being reported in various areas; by around 2010, the removal of deer had become widespread throughout Iwate Prefecture. Figure 2.3 shows the transition of the square root of the total area of the extermination and

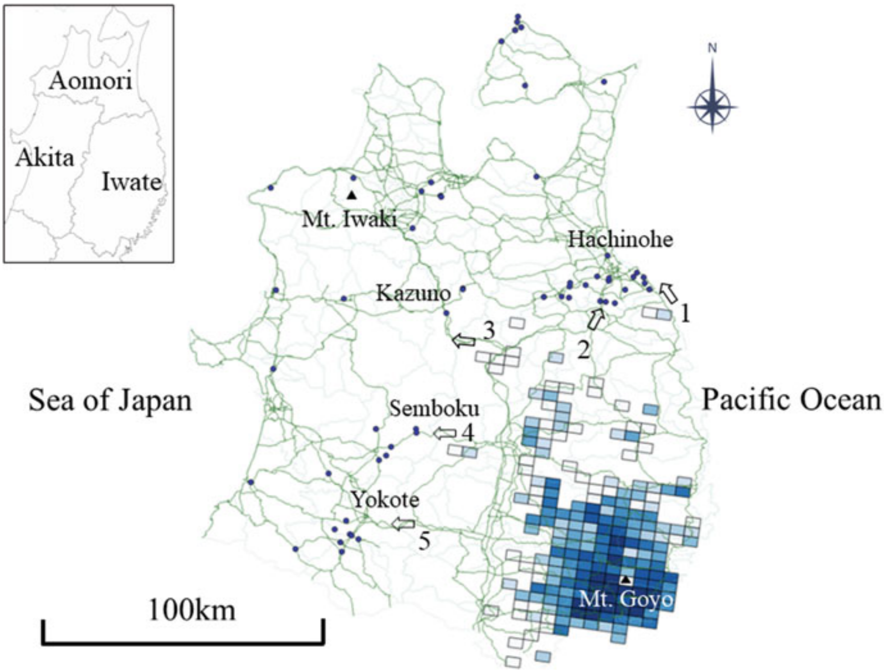

Fig. 2.4 Record of sika deer in northern Tohoku as of 2012. The border between the three prefectures is mountainous, and the major road (*thin lines*) passes through an area of low elevation. The grid in Iwate Prefecture indicates the areas where sika deer are culled; the darker the color, the greater the number culled. Black dots indicate locations of information on deer sightings or collisions between deer and traffic from 2005 to 2012 for Aomori Prefecture and from 2009 to 2012 for Akita Prefecture. One can predict that the population originating from Mt. Goyo has invaded Aomori and Akita prefectures through the lower elevations of the prefectural borders (*arrows* No.1 –No. 5)

capture in Iwate Prefecture from 2000 to 2011, indicating a positive slope, as seen in the nationwide expansion process (Fig. 2.2).

In neighboring Aomori and Akita prefectures, sika deer have been spotted since 2005 and 2009, respectively. Where did these deer come from? There are three possible explanations: (1) sika deer living in Hokkaido (Ezo sika deer) crossed the sea, (2) sika deer escaped from a deer farm, and (3) sika deer invaded from Iwate Prefecture. The results of DNA analysis of fecal pellets have revealed that there were many individuals from the area around Mt. Goyo in Iwate Prefecture (Yamada et al. 2019), and the expansion of the deer distribution in Aomori and Akita prefectures is likely a result of invasion from Iwate Prefecture; however, the other two possible explanations cannot be ruled out entirely. The sika deer that conquered almost all of Iwate Prefecture expanded their distribution to neighboring Akita and Aomori prefectures.

The process of expansion of sika deer in the northern Tohoku region is shown in Fig. 2.4. The number of deer captured in Iwate Prefecture has been calculated using the regional grid. The number of deer captured in 2012 is shown in the figure by the shading of the color. Hunting has not begun in both Aomori and Akita prefectures, and each point is a plot of eyewitness information collected from 2005 to 2012 in Aomori Prefecture and from 2009 to 2012 in Akita Prefecture and recorded without distinction between sexes. Although eyewitness information can be obtained only where there is an overlap between deer habitats and human activity, it may be possible to estimate the route of immigration. Deer invasion from Iwate Prefecture must be more likely to occur at lower elevations than at any point in the backbone of the Ou Mountains. People also use this route to travel between Iwate and the other two prefectures. Although the deer do not seem to enter directly via the roads or tracks, this route of entry may not be far from the truth. Based on the sighting information points plotted, the deer that were spread all over Iwate Prefecture may have used the five routes shown in the figure to enter Aomori and Akita prefectures.

In considering the expansion of deer distribution, it is important to distinguish between male and female deer. During estrus in autumn, the males are active and expand their home range greatly, so it is not a cause for concern to see them where deer have not been seen before. Where deer have never been, there is plenty of food and little fear of damage. As females do not wander in this fashion, the presence of females means that the deer have settled there, i.e., they have overwintered and bred, and their range of distribution has expanded gradually. Records show that the first female invaded Aomori Prefecture in 2011, the first to invade Akita Prefecture was in 2013, and approximately 5 years had passed since the first male was confirmed in both prefectures. The distribution of female deer expanded in Aomori and Akita (approximately 132 and 124 km from Mt. Goyo) at a rate between 7.3 and 8.8 km per year, respectively.

Figure 2.5a, b, c, and d show the invasion process in Aomori and Akita prefectures, focusing on females only. Figure 2.5a indicates the locations of females confirmed up to 2014. Given subsequent trends (Fig. 2.5b, c, d), it appears that females have invaded three areas, respectively. An increase in the number of eyewitnesses in each area may be due to continuing invasion or invading individuals reproducing, giving birth to the next generation, and gradually increasing their home range. In any case, this indicates the establishment and expansion of action by deer in the region, and there is great concern about future damage to agricultural and forestry crops. Calculating the distribution area based on the observed points in every year, the square root of the total area of both males/females and only females are regressed to a positive slope in the same way as the nationwide expansion process (Fig. 2.2) and the expansion process of the capture area in Iwate Prefecture (Fig. 2.3) throughout years.

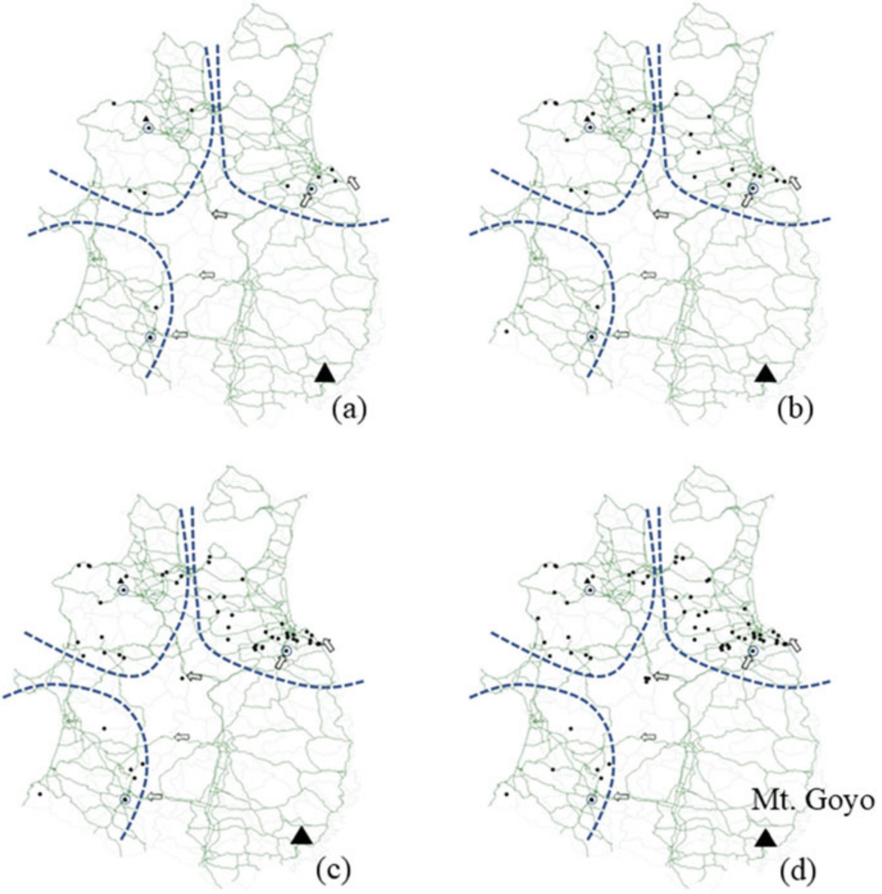

Fig. 2.5 (**a, b, c, d**) The record of female sika deer in Aomori and Akita as of 2014 (**a**), 2015 (**b**), 2016 (**c**), and 2017 (**d**). The area invaded by the female deer can be subdivided into three main areas (*dotted lines*). The three circled points indicate the location of the first confirmed female in the area with one recorded in the southern part of Hachinohe in 2011 and one recorded in the southern foot of Mt. Iwaki and Yokote in 2013. Solid lines indicate the main road network

2.3 Importance of Citizen Science in Monitoring: Deer Information Map

"Deer Information Map (https://shikadoko.animalenq.jp/)" is a web GIS system (information map viewed by portable terminal) that has been developed and implemented nationwide through collaboration between the Aichi Forestry Research Institute, MapQuest Corporation, and the Forestry and Forest Products Research Institute, granted by Agriculture, Forestry, and Fisheries Research Council (JPJ006258). Not only local government officials but also residents, hikers, nature lovers, forestry and agricultural workers, members of hunting associations, and researchers themselves can access deer sighting information in an integrated manner and share the information. For example, the system will make it possible for hunters to find the most efficient places to cull deer and for local government officials to speculate the areas that should be focused on.

This is one of the advantages of using GIS in a community, and the system has become an indispensable information infrastructure for modern society. Moreover, as the population of Japan continues to decrease, it will become increasingly difficult to gather information on the habitats of wildlife in mountainous areas. It is extremely difficult for individual researchers and government officials to collect such information on their own. Although there have not been many individual eyewitness information accounts, the value of such reports increases dramatically when they are aggregated.

Past records collected by each prefecture have already been entered, and anyone can add eyewitness information at any time. The system works on mobile devices such as Android and iOS, in addition to PCs. It is very easy to use; when the user selects “deer sighting report” from the top page, a map of the user’s current location is displayed, and the user can select the gender (male, female, and unknown) and the number of deer seen from the pulldown menu and submit these data. The system has been made so simple because users will be more reluctant to use it if they have to provide more detailed sighting information. In such citizen science, never asking too many questions is the key to continuing to gather information over a wide area and over a long period of time. From the autumn of 2020, even if the current user location is outside the service area, the information entered will be waiting for transmission and will be transmitted automatically as soon as the user enters the service area. There is also a “browsing page” where users can see what other people have reported, in addition to their own reports. This is where the sharing of information about sika deer begins. The deer information map as a form of citizen science has just begun, and its effective use in the future is highly anticipated. The data from the deer information map could also be utilized in scientific analysis. The use of such data, collected over a short period of time and over a wide area, may change the concept of the rate of expansion of the distribution of the deer, as discussed earlier.

Since ancient times, people in various parts of Japan have encountered deer. The balance between humans and deer began to deteriorate following World War II, and legal protection has allowed deer to demonstrate their unparalleled fertility fully, increase their population sizes, and expand their distribution. The route of the expansion of deer distribution is a cluster of heterogeneous habitats, and there must be both suitable and unsuitable habitats for deer. For instance, on the north side of Mt. Goyo, the development of grass farming that began in 1976 in the Kitakami Mountain range has remained the abandoned pastureland, which would have promoted expansion of the distribution of the deer (Noda et al. 2013). Conversely, the Kitakami River running north-south along the west side of the Kitakami Mountain range, the Tohoku Expressway, the national highway, and railroad lines running along the river must have changed the direction of expansion of the deer distribution, but they have not inhibited it.

Empirically, we can state that strengthening trapping in each region is the only way to halt or even slow down the expansion of distribution of the deer. People concerned in affected areas will be needed to share information on deer distribution with prefectures and municipalities, actively evaluate current damage control measures, determine capture locations, and create adaptation measures to minimize the impact of increased distribution. Sharing information on deer among government, local residents, and sometimes researchers and finding solutions based on this information are the best way to adapt to the expanding distribution of deer.

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Chapter 3
The Impact of Sika Deer on Vegetation in Japan

Haruka Ohashi

Abstract The Japanese archipelago is long and narrow from south to north, and vegetation zones are distributed according to a wide range of climates, from subtropical in the south to subarctic in the north. In such a diverse environment, about 7500 species of vascular plants grow, of which about 36% (about 2700 species) are endemic (Kato and Ebihara, Endemic plants of Japan. Tokai University Press, Tokyo, 2011). In recent years, the high density of deer has become a major problem in conserving these diverse plants in the Japanese archipelago. Sika deer are widely distributed in Japan, from Yakushima Island in the south to Hokkaido Isl. in the north (Biodiversity Center of Japan, Ministry of the Environment, The second national survey on the natural environment: report of the distribution survey of Japanese animals (mammals), 1979; Biodiversity Center of Japan, Ministry of the Environment, The sixth national survey on the natural environment: report of the distribution survey of Japanese animals (mammals), 2004), in vegetation zones ranging from warm-temperate evergreen broad-leaved forest zones to subarctic and subalpine evergreen coniferous forest zones and alpine zones. The impact of deer on vegetation, regardless of its nature, is apparent in various vegetation types, from forests to grasslands, and has a variety of effects. In this chapter, I will briefly describe the major vegetation zones in Japan. After that, I will review the effects of high deer densities on vegetation throughout Japan. Then, I will introduce the currently reported impacts of deer on each vegetation type.

3.1 Brief Introduction of Vegetation in Japan

The Japanese archipelago stretches 3000 km long, forming a narrow arc from south to north at the eastern coast of the Asian continent. Japan's flora is included in the Eastern Asiatic Region (also known as Sino-Japanese Region) within the Holarctic

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H. Ohashi (✉)
Department of Wildlife Biology, Forestry and Forest Products Research Institute, Tsukuba, Japan
e-mail: harukaohashi@affrc.go.jp

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Floral Kingdom, except for the Nansei-Shoto and Ogasawara Islands which belong to the Paleotropical Floral Kingdom. According to climatic changes at geological time scales, many plant species have been migrated from the Asian continent and have been less affected by glaciers. Therefore, some have evolved and speciated within this region, and some have become relict species protected by the ocean which constituted the uniqueness of vegetation in Japan.

Horizontally, this archipelago distributes from subtropical in the south to subarctic in the north, and vertical distribution almost corresponds to horizontal distribution from the coast to the alpine summit (Fig. 3.1a). All of this area experiences abundant precipitation throughout the year, allowing the establishment of the forest at the climax stage. To be more precise, precipitation seasonality differs on both sides of the central backbone mountains: the southeast monsoon wind in summer brings a large amount of rain on the Pacific Ocean side, and the northwest monsoon wind in winter brings a large amount of snow on the Sea of Japan side and in Hokkaido. Especially, the Sea of Japan side is one of the world's most heavy snow regions, which affect various aspects of vegetation, and forms the uniqueness of its flora. In such a diverse environment, about 7500 species of vascular plants grow, of which about 36% (about 2700 species) are known to be endemic (Kato and Ebihara 2011). This endemicity arises from two different types of origin: ancient relict endemics and new endemics. The former group was originally widely distributed in other regions and shrinks its distribution due to factors such as climate change and currently remains only in Japan. One of the reasons is that East Asia was generally not covered by ice sheets to the same degree as Europe and North America during the Ice Age and had been functioning as refugia for many late Neogene/Quaternary plant taxa (Tang et al. 2018). The latter group was species formed in Japan: for example, during repeated glacial and interglacial periods in the Ice Age, species were repeatedly immigrated from the continent and isolated and differently adapted to the regional environment. For example, species in genus *Sasa* have widely diverged in northern Japan, adapting to differences in snow conditions (Fig. 3.2). As a heavily populated, industrialized nation, this area still possesses high biodiversity and has been identified as one of the world's 35 Biodiversity Hotspots (Mittermeier et al. 2011).

In the main four islands of Japan (Kyushu, Shikoku, Honshu, and Hokkaido), four major climatic vegetation zones can be recognized: warm-temperate zone dominated by evergreen broad-leaved forest, cool-temperate zone dominated by deciduous broad-leaved forest, subalpine zone dominated by coniferous forests, and alpine zone above the timberline (Numata et al. 1972). Warm-temperate zone is defined as the area where the warmth index (WI; WI = sum of $(T_m - 5)$ when T_m is above 5 C° (T_m: monthly mean temperature), Kira 1948) is 85°C/month or higher (Kira 1948) and covers the largest area in Japan (Oono 2005). Generally, evergreen broadleaf trees dominate at climax stage. Major tree species are *Machilus thunbergii*, *Castanopsis sieboldii* in coastal areas, and *Quercus glauca*, *Q. gilva*, *Q. salicina*, *Q. myrsinifolia*, and *Q. acuta* in inland areas. In general, characteristic species in evergreen broad-leaved forests are more abundant in the warmer southern regions, and the number of such species decreases as they move northward (Hattori et al. 2002). Some researcher subdivides this zone by coldness index (CI: CI = − sum of

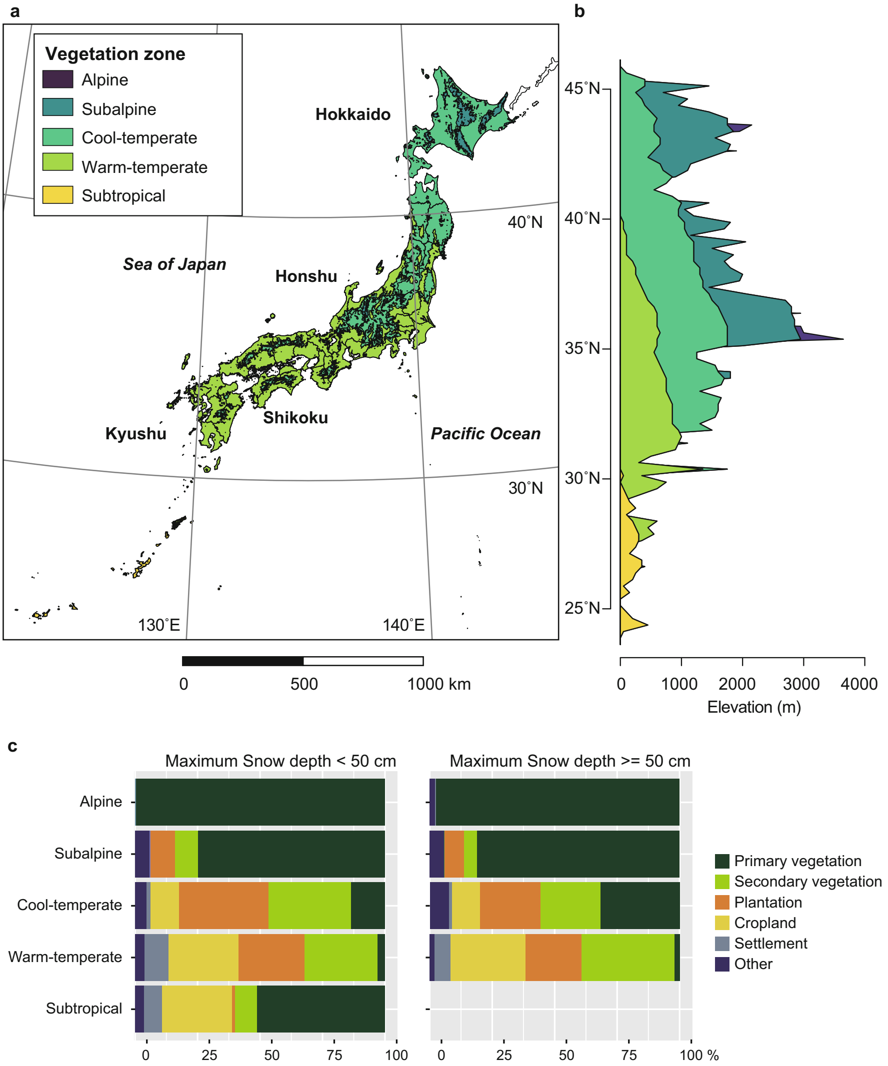

Fig. 3.1 Horizontal and elevational distributions of the vegetation zones in Japan. (**a**) Horizontal map; (**b**) Elevational distribution. The boundary line in the map represents the prefectural border. (**c**) Land use by humans in each vegetation zone. Map and calculation were based on data from Ministry of Land, Infrastructure, Transport, and Tourism of Japan (2021a, b), Ogawa et al. (2013) and Akasaka et al. (2014)

($5 - T_m$) when T_m is below 5 C°, Kira 1949) of -10°C, the limit of evergreen broadleaf tree species, and distinguishes “meso-temperate zone” dominated by *Fagus japonica*, *Q. serrata*, *Abies firma*, and *Carpinus* spp. in the sub-zone with CI < -10°C/month (Nozaki and Okutomi 1990).

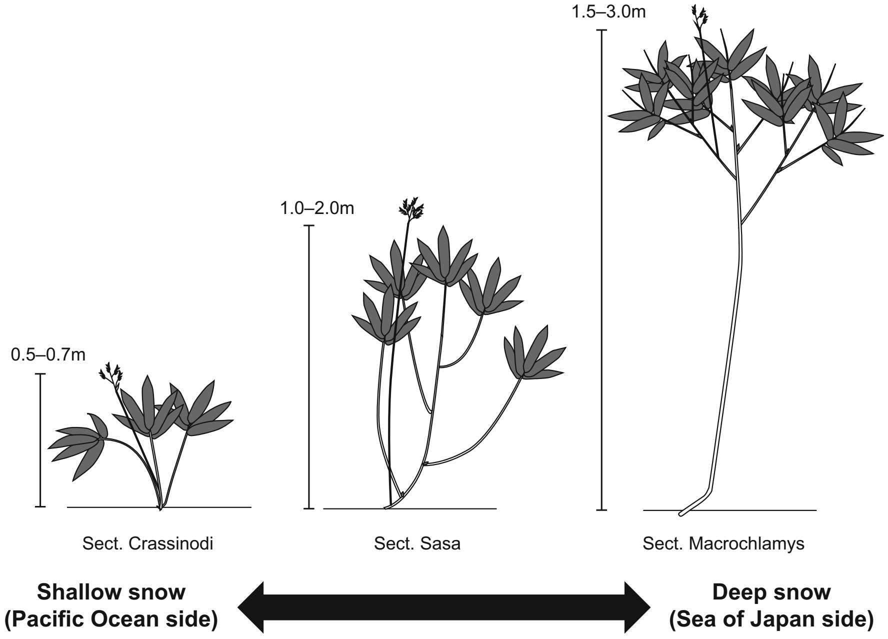

Fig. 3.2 Schematic diagram of the morphological difference in genus *Sasa* in response to maximum snow depth. *Sasa nipponica*, which distributes on Pacific Ocean side, is belonging to the section Crassinodi, and *Sasa kurilensis*, which distributes on the Sea of Japan side, is belonging to the section Macrochlamys. Created by the author based on the figure of Suzuki (1996) with modifications

In the cool-temperate zones of Japan (WI 45°C/month or higher and below WI 85°C/month), forests dominated by deciduous broad-leaved trees are established (Kira 1948). The dense growth of dwarf bamboo (*Sasa* spp.) on the forest floor is a unique characteristic of the Japanese cool-temperate zone. The main dominant trees are *Fagus crenata*, *Kalopanax septemlobus*, *Tilia japonica*, *Q. mongolica* var. *grosseserrata*, *Magnolia obovata*, and so on. Species composition of these forest differs according to snow depth gradients: forests on the Sea of Japan side with heavy snow are characterized by *Sasa kurilensis*, *Acer japonicum*, *Hugeria japonica*, and evergreen shrub such as *Aucuba japonica* var. *borealis*, *Daphniphyllum macropodum* var. *humile*, *Cephalotaxus harringtonia* var. *nana*, and *Skimmia japonica* var. *repens*, which have ecological advantage in the photosynthetic activity soon after the snow melts. On the other hand, the Pacific Ocean side is characterized by *S. borealis*, *A. sieboldiana*, *Stewartia pseudo-camellia*, *S. nipponica*, etc. Moreover, many relict endemic genera and species of Japan grow in this zone, and many of those are relict floras developed in late Neogene/Quaternary that are closely related to the mountainous regions of south-central China.

In the subalpine zones of Japan (WI 15°C/month to WI 45°C/month), evergreen coniferous forests are established (Kira 1948). The subalpine zone of Honshu and

Shikoku is dominated by *Abies mariesii*, *A. veitchii*, *Tsuga diversifolia*, and *Thuja standishii*, while same climatic zone of Hokkaido is dominated by *Picea jezoensis* and *A. sachaliensis*, accompanied with *Picea glehnii*. In the areas where coniferous trees are prevented from becoming taller, such as windblown areas, cliffs, avalanche areas, areas with a long period of snow cover, and ultrabasic rocky areas, deciduous shrublands are dominated by *Betula ermanii* and *Alnus alnobetula* subsp. *maximowiczii*, and grasslands with a variety of tall-stemmed broad-leaved herbs, such as *Trollius shinanensis* and *Ranunculus acris*, are locally established.

Although most parts of Japan do not reach the climatic timberline, there is distinct timberline close to the summit by climatic stress such as strong wind and heavy snow. In the alpine zone above the timberline, various habitats exist as mosaic patterns reflecting topographic condition, which affects snow distribution and soil moisture on a microscale. Most of the various types of plant communities establish according to those microhabitats, such as *Pinus pumila* thickets, snow-patch vegetation with *Sieversia pentapetala* on the downwind slope where snow accumulates, and dwarf shrub communities with *Loiseleuria procumbens* and *Vaccinium ovalifolium* on the upper part of the windward slope. Such alpine vegetation is extremely fragile and difficult to recover once it has been destroyed.

Although most of Japan has the potential to forest establishment, some parts are edaphically not, such as mires, a grassland-like landscape dominated by grasses and peat moss (*Sphagnum* sp.) which has developed on peat. Peat is a pile of decomposed plant remains that accumulates at a rate of about 1 mm per year. Peat requires several factors to form, such as wide lowlands that allow water to stagnate, plants as materials, and low temperatures that inhibit microbial activity and slow down decomposition. In Japan, the area of mire is larger in high latitudes, and 83.6% of all mires in Japan is distributed in Hokkaido, including Kushiro Mire and Sarobetsu Mire. The mires can be subdivided into fen and bog, according to their developmental stages. Fen is a type of peat-accumulating wetland fed by mineral-rich ground or surface water and generally consists of large herbaceous plants such as *Phragmites australis*, *Zizania latifolia*, and *Miscanthus sacchariflorus*. A bog is a mire system entirely dependent on precipitation for its water and solutes, as its surface raised above the water table due to the accumulation of undecomposed mossy peat. As different plant species grow according to microtopography and moisture environment, species composition of mire is usually complex and forms mosaiclike patterns of heterogeneous habitat.

Previous parts have outlined the vegetation in its original state without human disturbances; however, in reality, most of Japan's vegetation has been altered by humans since prehistoric times and replaced by croplands, residential areas, secondary forests, or plantations for timber trees. The most modified zones are warm-temperate zones, and the cold and snowy area still possesses large proportion of native vegetation (Fig. 3.1b). The long history of traditional management in the human-modified zone (such as periodic logging and removal of fallen leaves in forests) has contributed to sustaining a variety of sun-loving herbaceous plants growing in the understory of forests (Tsuji and Hoshino 1992). However, many forests have been left unmanaged recently due to the recent decrease in the demand for charcoal, firewood, compost, and humus (Yamaura et al. 2012).

Additionally, human activities such as grazing, harvesting, and burning can stop vegetation transition and maintain the grassland condition which is called secondary grasslands or seminatural grasslands (Tansley 1923). In the past, seminatural grasslands occupied a large area of Japan as pasture and grassland, but their area is rapidly decreased since the 1960s due to land development, coniferous plantations, and abandonment (Ogura 2006). In these grasslands, many common species with Asian continents (e.g., Korean Peninsula and northeastern China) distribute. These species are considered as migrants during the Ice Age, when the Korean Peninsula and Japan were connected by land, and then remained as remnants in the grasslands due to volcanic and human activities. The decrease in managed grasslands has led to a decrease in the number of plants that prefer a sunlit environment, many of which have been designated as endangered species (Osawa et al. 2013).

3.2 Overview of Sika Deer Impact on Vegetation in Japan

Currently, sika deer are widely distributed from Yakushima Island in the south to Hokkaido in the north, which covers warm-temperate zone to alpine zones. The impact of deer on vegetation is observed in all four vegetation zones and has various effects according to population density.

Sika deer depend on plants as their primary food resource. Sika deer remove (and eat) leaves, stems, flowers, fruits, and other organs from the plant body during the browsing. Usually, these losses of the organ are detrimental for the plant, which result in smaller plant height and inhibit their reproduction (Anderson 1994). As the population density of sika deer increases, the amount of plant organ removed as forage also increases, resulting in the death of the individual or a population decline if flowering and fruiting are inhibited for an extended period of time (Knight 2003). Some plant species have evolved specific traits to avoid foraging. Some species defend themselves with toxic substances or thorns (unpalatable plants), while others can survive after foraging by increasing the number of leaves and photosynthetic capacity and by compensatory regrowth (foraging-tolerant plants).

The response to deer foraging varies among species, and these differences are essential for predicting the response of vegetation to changes in deer density. For example, species turnover is likely to occur when the browse intolerant species are weakened by frequent browsing, and other browse tolerant species establish in the gap created by the disturbance caused by the deer (see Fig. 3.3 for example of browse intolerant species in Japan). In the area with relatively low sika deer density, the dominance of highly competitive species may decrease, while smaller or more tolerant species may establish, resulting in the increase of species diversity compared to the areas without Sika deer (Suda and Koganezawa 2002; Suzuki et al. 2008; Suzuki et al. 2013). However, when the sika deer density becomes high, the growth of many browse intolerant species becomes difficult, and only a limited number of

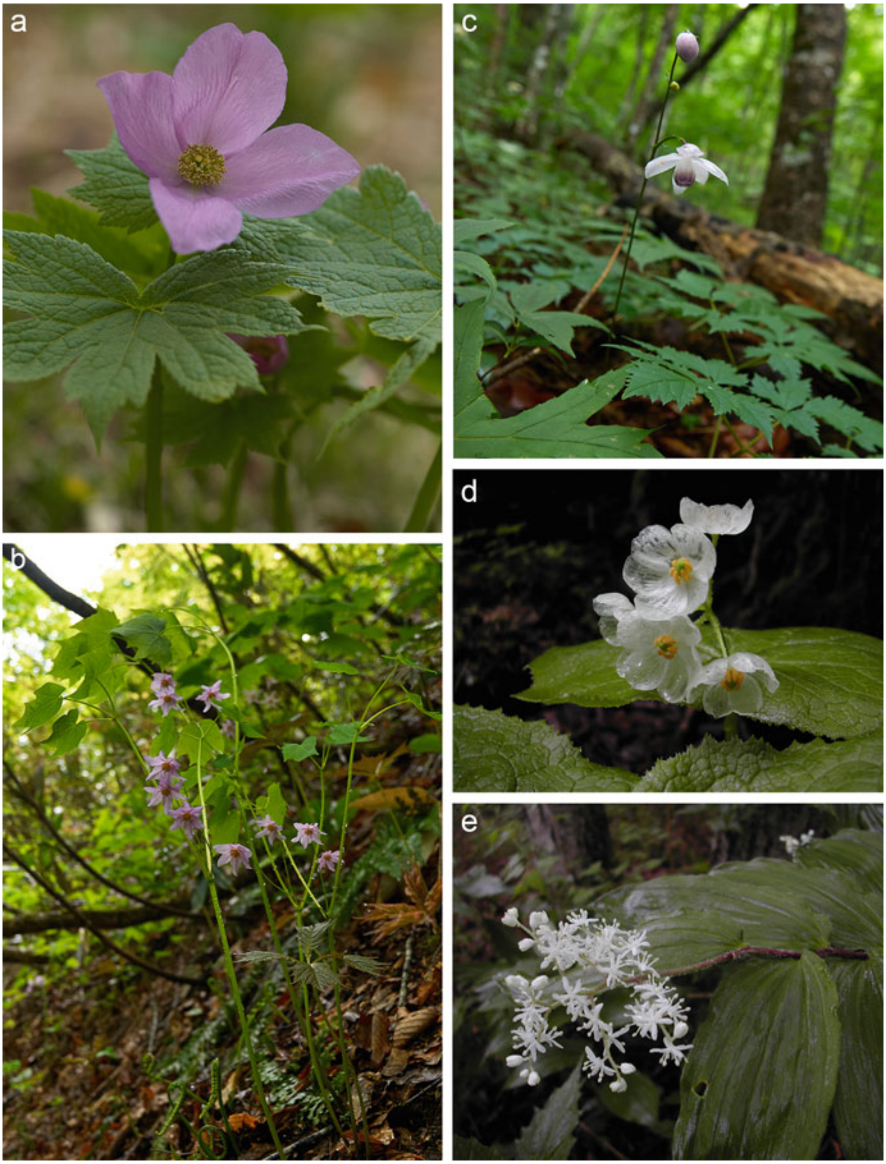

Fig. 3.3 Examples of plants which are vulnerable to browsing of sika deer. (**a**) *Glaucidium palmatum* (endemic), (**b**) *Ranzania japonica* (endemic), (**c**) *Anemonopsis macrophylla* (endemic), (**d**) *Diphylleia* grayi, (**e**) *Maianthemum robustum* (endemic). (**a**, **b**, **c**: photo by Koji Ohashi; **d**, **e**: photo by Haruka Ohashi)

unpalatable or foraging-tolerant plants can grow, resulting in a significant decrease in species diversity. Not only feeding by deer but also trampling and digging can have a great impact. For example, in Kushiro Mire, the effects of trampling and disturbance by deer have been reported to reduce the cover of dwarf shrubs and mosses, create the bare ground, and invade annual herbaceous plants (Muramatsu and Fujita 2015). The destruction of microtopography in these vulnerable plant communities has a particularly large impact and takes many years for the vegetation to recover.

Generally, in areas with high deer densities, medium- to large-sized herbaceous plant (>30 cm) and shrub species are especially likely to disappear (Ohashi et al. 2007; Hattori et al. 2010; Otsu et al. 2011; see Fig. 3.3 for some example). This is because these species need to complete their life cycle within a space lower than the height of the deer's mouth, which suffers the most intense browsing pressure. Additionally, studies comparing the inside and outside of deer-proof fences have shown that species with larger leaf areas and higher chlorophyll content increase inside fences (Nishizawa et al. 2016), suggesting a certain trend in functional traits of species vulnerable to deer browsing pressure.

Selective loss of species with specific traits may also have important consequences for ecosystem functioning. For example, medium to large herbaceous species and shrubs growing in the forest understory are known to contribute to water source recharge functions such as trapping litter, reducing soil surface drying, maintaining soil infiltration capacity, and mitigating soil erosion (Sakai 2013). When the understory vegetation declines due to high deer densities, litter is more likely to move, reducing the forest floor cover and consequently accelerating soil erosion (Chaps. 23 and 27). When the basis of ecosystems is altered by heavy deer browsing pressure, irreversible changes may occur that cannot be restored to the original state (Royo et al. 2010; Tanentzap et al. 2012).

In Japan, vegetation change by heavy browsing pressure of sika deer has long been observed in areas close to old shrines, where deer have been protected as a messenger of gods, such as Kinkazan Island and Nara Park (Yoshii and Yoshioka 1949; Yoshioka 1969). However, at that time, the heavy impact of sika deer on vegetation was believed to occur only in the specific conditions, and few ecologists at that time expect that sika deer densities would increase in the near future and cause a drastic impact on vegetation throughout Japan. In the late 1980s, reports of the effects of high deer densities on vegetation began to appear in Mt. Odaigahara (Hoshino et al. 1987), the Boso Peninsula (Kabaya 1988), and Mt. Nikko-Shiranesan (Hasegawa 1992, 2000). In the late 1990s, the number of reported cases increased rapidly, mainly on the Pacific Ocean side (Akashi and Nakashizuka 1999). In recent years, the effects of deer on vegetation have also been reported on the Sea of Japan side, an environment with heavy snowfall (Tanaka et al. 2008; Fujiki et al. 2011). The first nationwide survey on the impact of sika deer on vegetation was conducted by the Planning Committee of the Society of Vegetation Science in 2009–2010 (Planning Committee of the Society of Vegetation Science 2011). The purpose of this survey was to collect information evenly throughout the country, and it was conducted with the voluntary cooperation of 154 people with basic knowledge and skills about vegetation in various parts of Japan (Fig. 3.4). Statistical analysis using the data obtained from this survey attempted to extract the characteristics of the areas where the effects of deer were most likely to become apparent (Ohashi et al. 2014).

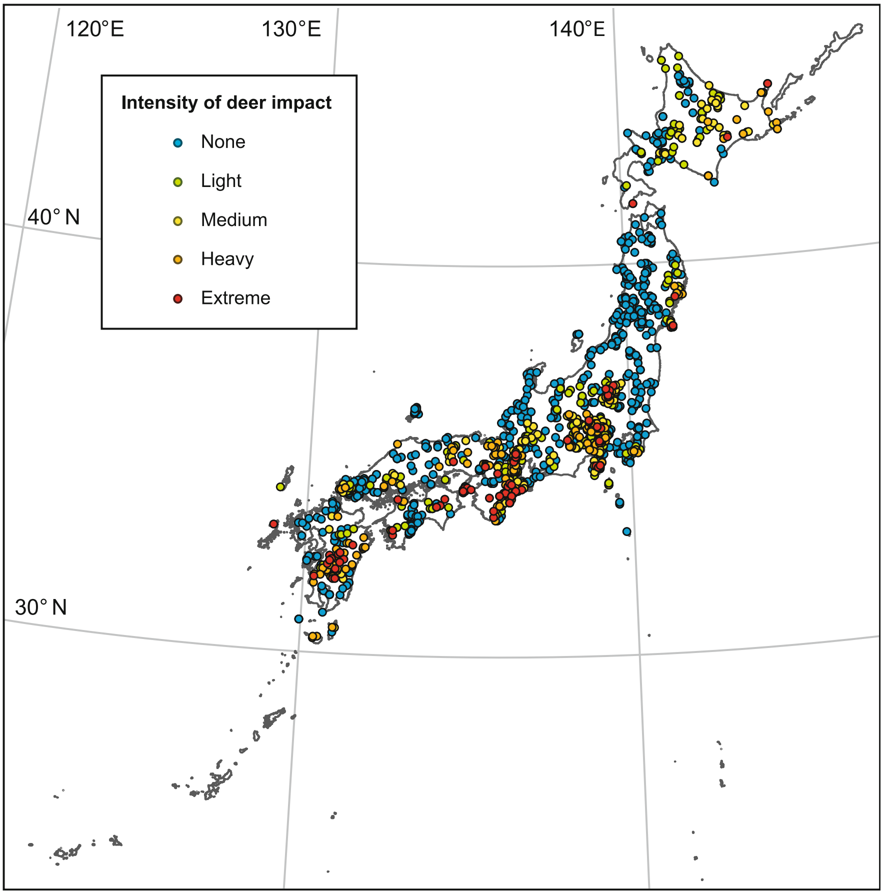

Fig. 3.4 Geographical distribution of sika deer impacts on vegetation across Japan as revealed by the Sika Deer Impact Survey, 2009–2010 (reprinted from Ohashi et al. 2014)

As a result, the areas with the most substantial impacts were found to be those where the following three conditions overlapped: "surrounding areas where the sika deer have inhabited continuously for a long time," which possibly reflects both density and cumulative effect, "the snow cover period is short", which reflects wintering range, and "area without urban areas," avoidance of intense human disturbance (Fig. 3.5). In 2018–2019, a second nationwide survey on the impact of sika deer on vegetation was conducted (Maesako et al. 2020). Detailed analysis is currently underway, but it was clear that the area under the heavy impact of sika deer has increased in these 10 years, the Pacific Ocean side of Japan and expanding into inland and the Sea of Japan side.

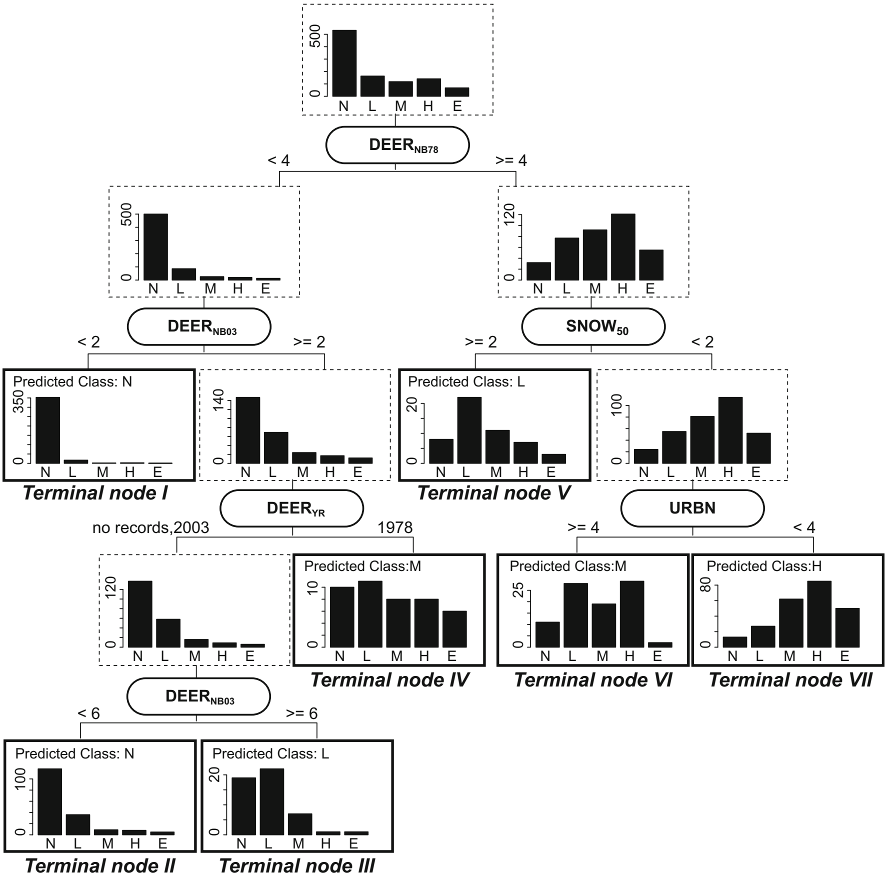

Fig. 3.5 Decision tree for the CART model built using data from the Sika Deer Impact Survey In each partition; the value of the splitting variable is shown. The terminal node is illustrated by a bold box. Information featured in the terminal nodes includes the level of the predicted intensity class. The number of grid cells for each intensity class within the node is displayed as a bar plot. N, none; L, light; M, medium; H, heavy; E extreme (reprinted from Ohashi et al. 2014)

3.3 Detailed Information of the Deer Impact in Each Vegetation Zone

3.3.1 Deer Impacts on Warm-Temperate Zone Vegetation

In the warm-temperate zone, detailed studies of the impact of deer on vegetation have been conducted in Yakushima Island (Koda 2017), Tsushima Island (Suda and Koganezawa 2002), and Chiba Experiment Forest, University of Tokyo (Kabaya 1988). Although most existing studies have been conducted in secondary forests, some detailed studies have been conducted in the primary forest. For example, in the primary evergreen broad-leaved forest in the Aya town, Miyazaki Prefecture, a detailed comparison was made with data from a vegetation survey conducted in 1988, before the increase in the number of sika deer in a forest relatively close to its original state (Hattori et al. 2010). According to this study, in 2009, a significant decrease in vegetation cover was observed in the shrub and herbaceous layers below 2 m in height, such as *Damnacanthus indicus* var. *major*, *Elaeocarpus japonicus*, *Rubus buergeri*, and *Alpinia japonica*. Moreover, while characteristic species of evergreen broadleaf forests, such as *Trachelospermum asiaticum* var. *asiaticum*, have decreased, forest edge and sun-loving species *Callicarpa japonica* and *Celtis sinensis* have newly appeared on the forest floor cleared by deer foraging. Totally, the number of species that have decreased or disappeared with the increase in the density of deer greatly exceeds the number of species that have increased or newly emerged, suggesting that species diversity has become significantly simpler. In this region, additionally to the changes in the species composition, concerns about negative impacts on the endangered plants such as *Apostasia nipponica* and *Sciaphila nana*, which specifically grow in primary evergreen broadleaf forest, were raised by plant taxonomists (Society of Plant Taxonomists of Japan 2003).

Evergreen broad-leaved forests close to their original state are left in the territory of shrines and temples. However, even in these forests, the impact on vegetation by sika deer has been reported (Ozaki et al. 2013). In the Kasugayama Primeval Forest in Nara Prefecture, which is close to urban areas, deer-unpalatable plants, such as the non-native foreign species *Triadica sebifera* and the non-native domestic species *Nageia nagi*, have invaded from planted individuals in nearby parks, replacing the native forest species (Maesako et al. 2007).

3.3.2 Deer Impacts on Cool-Temperate Zone Vegetation

In the cool-temperate zone, the impact of sika deer on vegetation has been reported before the 1990s, mainly on the Pacific Ocean side. In the Tanzawa Mts. in Kanagawa Prefecture, the massive dieback of *Sasa borealis* due to heavy deer browsing had firstly observed between 1973 and 1980. Since then, *Sasa borealis* declined over several thousand hectares by the 1990s (Furubayashi and Yamane 1997). Similarly, the massive dieback of *Sasa borealis* has been reported in other regions of the Pacific Ocean side of the cool-temperate zone (Koizumi et al. 2006; Ohashi et al. 2007), which suggests that this phenomenon is common throughout Japan. In addition, the impact on shrubs and herbaceous species other than *Sasa borealis*, which mainly grow in the mountains in the cool-temperate zone, has been significant. Until the 1980s, forests dominated by various broad-leaved herbaceous species had developed in valley forests dominated by *Fraxinus platypoda* and *Pterocarya rhoifolia* or in cloud forests established on gentle slopes and volcanic ash soils dominated by *Fagus crenata*. However, in areas with high deer densities, many of these broadleaf herbs can only be found in fences and facing the danger of disappearing after the late 1980s (Tamura et al. 2005). For example, in the central mountains of Kyushu, the communities of *Kirengeshoma palmata* and *Comanthosphace stellipila* var. *tosaensis*, which grow mainly in natural forests in the cool-temperate zone, are reported to have almost disappeared (Kumamoto Prefecture 2009).

Although there are relatively few reports of deer impact on the Sea of Japan side of the cool-temperate zone, in the Ashiu Research Forest of Kyoto University, the number of sika deer increased dramatically in the 2000s, causing the decline of the *Sasa kurilensis* and *Cephalotaxus harringtonia* var. *nana* on the forest floor (Tanaka et al. 2008). In this area, despite the relatively low population density of deer, evergreen plants are subjected to intensive foraging during the winter, when leaves are accessible to deer, resulting in the decline of these plants. In Hyonosen, located on the Hyogo and Tottori prefectures' border, browsing mark of sika deer was found on 230 species, including 13 endangered plant species. Especially, there is concern about the impact of deer feeding on large cool-temperate herbaceous species with a central distribution range north of the central part of Japan, such as *Caltha palustris* var. *enkoso* and *Miricacalia makinoana* (Fujiki et al. 2011). In the cool-temperate zone, changes in forest floor vegetation cover due to high deer densities have been reported to progress in a few years (Fujiki et al. 2011), and early countermeasures are considered necessary.

3.3.3 Deer Impacts on Subalpine Zone Vegetation

In the subalpine zones, studies on the effects of bark stripping on forest canopy species have been conducted in Odaigahara (Hoshino et al. 1987; Akashi and Nakashizuka 1999), Mount Fuji (Takeuchi et al. 2011), the Southern Japan Alps (Iijima and Nagaike 2015), and Nikko, Tochigi Prefecture (Kanzaki et al. 1998). However, a lack of literature clarifies how the forest floor vegetation in subalpine coniferous forests has changed with the increase in the sika deer population. In the Okutama-machi in Tokyo metropolitan, the cover of broadleaf shrub growing in the understory, such as *Rhododendron pentandrum*, has significantly decreased between 1980–1985 and 1999–2004; even the forest canopy was not significantly affected (Ohashi et al. 2007). They also reported that while large plant species such as *Dryopteris expansa* and *Streptopus streptopoides* subsp. *japonicus* decreased, small herbaceous species such as *Oxalis acetosella* were relatively unaffected.

In Odaigahara, Nara Prefecture, the forest floor environment has changed significantly since the 1960s, after dieback of *Picea jezoensis* var. *hondoensis* and *Abies homolepis* due to bark stripping by deer. Before the 1960s, the forest floor in this forest was covered by carpet-like mosses. However, after the dieback of standing trees, light-loved *Sasa nipponica* expanded their range and became the dominant species in the understory (Ando et al. 2006; Yokota 2009). Small herbaceous species which characterize the subalpine coniferous forests often grow in association with mosses, and when the moss layer declines, other species growing in the same area may be severely affected. Therefore, even in areas where the lower moss layer has not been significantly affected, it is necessary to monitor the situation carefully.

The impact on shrublands and grasslands in the subalpine zone is also serious. At Mt. Nikko-Shiranesan, various shrub and herbaceous species, such as *Salix reinii* and *Vaccinium ovalifolium*, which grew in the shrublands, or *Glaucidium palmatum* and *Pedicularis yezoensis*, which grew in the tall-stemmed grassland, were drastically reduced by deer browsing in the early 1990s (Hasegawa 1992, 2000). In the Omine Mountain in Nara Prefecture, *Magnolia sieboldii* subsp. *japonica*, which grows in avalanche-prone areas, has been declining due to deer predation.

In mire, various plant communities are established according to the microtopography and moisture environment, and foraging by sika deer, but also trampling and digging, has an enormous impact. The destruction of microtopography has had a particularly large impact on these plant communities and requires many years for recovery (Fujita et al. 2012; Muramatsu and Fujita 2015). In Honshu, the impact of deer has also been reported in Oze and the formation of bare ground by foraging and digging up the roots of Japanese honeysuckle (*Lonicera japonica*) and using it as a rutting ground, as well as the impact of foraging on *Hemerocallis middendorffii* var. *esculenta*, *Lysichiton camtschatcensis*, and *Caltha palustris* var. *nipponica* (Naito and Kimura 1998). According to Yoshikawa et al. (2021), changes in species composition were detected over 50 years, especially in the fen communities and shrub/forest communities compared to the fen-bog transition and bog communities. Additionally, similarity among different communities increased, suggesting the reduction in beta diversity across the wetland vegetation.

3.3.4 Deer Impacts on Alpine Zone Vegetation

In the alpine zone, tall-stemmed herbaceous communities and snowfield communities are severely affected. In the Southern Japan Alps, located on the border of Yamanashi, Nagano, and Shizuoka prefectures, deer have severely affected the vegetation of tall-stemmed herbaceous communities in the subalpine to alpine zones and snowfield communities (Nagaike 2012) resulting in the disappearance of *Cypripedium yatabeanum* and *Cypripedium macranthos* var. *macranthos* (Motoshima 2010). On the other hand, there is relatively little browsing damage in *Pinus pumila* forests: however, it is known that they are vulnerable once browsed and susceptible to dieback when the tops are eaten (Motoshima 2010).

At Yubari-dake in Hokkaido, which is known as a treasure house of alpine flora, deer have been seen since around 2006, and feeding damage to *Anthoxanthum pluriflorum* var. *pluriflorum*, an endemic plant of Yubari-dake, has been confirmed. Additionally, in Kirigishi-yama close to the Yubari-dake, deer browsing marks on *Cypripedium macranthos* var. *macranthos* were recently observed. According to the results of a camera trap survey conducted in 2010–2011, deer are already using the alpine zone as a summer feeding ground, which suggests the urgent need to take protection measures before the sika deer impact becomes serious (Sugiura et al. 2014).

3.3.5 Deer Impacts on Secondary Vegetation

In secondary forests in areas of high deer density, the shrub and herbaceous layers are severely declined under the high density of sika deer (Fujiki et al. 2006; Ishida et al. 2010). For example, in Hyogo Prefecture, shrub species such as *Toxicodendron trichocarpum* and *Lyonia ovalifolia* var. *elliptica*, and many herbaceous species such as *Aster scaber* and *Deyeuxia brachytricha*, do not appear in the secondary forest with high deer density, and appearance of *Illicium anisatum* is characteristic in such forest, with total species diversity significantly declining (Ishida et al. 2010). In addition, foraging of sika deer is known to cause the decline of the *Erythronium japonicum* community and inhibited its growth (Yamase et al. 2005).

Similarly, secondary grasslands are also severely impacted by the sika deer. Otsu et al. (2011) tracked changes in secondary grasslands in the mountain and subalpine zones of central Japan over a 30-year period and found that changes in species composition were greater in areas where deer more heavily used grasslands. As the impact of deer intensification increased, medium to large herbaceous species decreased, bare ground formed, and small herbaceous and woody species, graminoids increased. Therefore, once the grassland regresses due to the impact of intensity, the installation of deer fences in the area may promote the invasion of woody species. In Kirigamine, Nagano Prefecture, although the impact on the species composition of the grasslands is relatively small, the decline of *Hemerocallis middendorffii* var. *esculenta* and *Hemerocallis citrina* var. *vespertina*, which are tourism resources, has been observed, especially in areas that are not accessible to tourists (Ozeki and Kishimoto 2009). In order to maintain species diversity in secondary vegetation (both forests and grasslands) distributed in areas with high deer densities, it is necessary to implement measures that combine vegetation management such as mowing, logging, and litter removal with the reduction of deer density.

3.4 Conclusion

As described in previous sections, the rapid increase in the population of sika deer is now changing the vegetation of the entire Japanese archipelago. Then, how much of the natural vegetation is left undisturbed by sika deer? According to Ohashi et al. (2014), the history of sika deer distribution was the most important factor in determining the current intensity of deer impact (Fig. 3.5). When we aggregate the area of overlapping vegetation zones by the observation year of sika deer, more than 60% of natural vegetation at the Pacific Ocean side above the cool-temperate zone

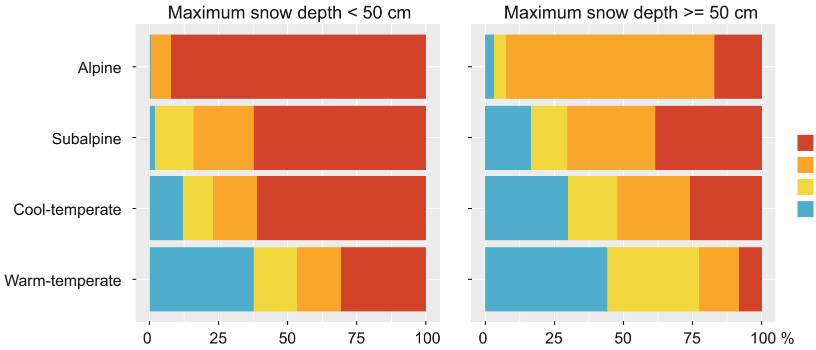

Fig. 3.6 First observation year of sika deer in natural forests in each vegetation zone in scarce snow area (left) and heavy snow area (right). Calculation was based on data from the Ministry of Land, Infrastructure, Transport, and Tourism of Japan (2021b); Biodiversity Center of Japan, Ministry of the Environment (1979, 2004); Ministry of Environment (2015); Ogawa et al. (2013); and and Akasaka et al. (2014)

had been overlapped with sika deer distribution in 1978 (Fig. 3.6). If we consider the persistence period of sika deer as a proxy of the current intensity of deer impact on vegetation, the result can be interpreted as more than 60% of natural vegetation at the Pacific Ocean side above the cool-temperate zone is now facing at risk of severe impact by sika deer. Before the 1970s, deer had been extensively hunted in areas that were easily accessible to humans and were distributed only in deep mountains with scarce snow. The decline in hunting pressure after the 1970s may have contributed to an increase in the population number of sika deer, which has been accompanied by an increase in population density in the core area of sika deer distribution and range expansion into the margin of the distribution. As a result, much of the natural vegetation on the Pacific Ocean side, which had overlapped with the historic core area of sika deer distribution, becomes to be severely affected by increased population pressure. Recently, sika deer have become increasingly distributed in natural forests on the Sea of Japan side, where there is heavy snow. Range expansion into the area with heavy snow is likely to be accelerated by climate change in the future due to a decline in snow cover period (Ohashi et al. 2016). Moreover, not only the distribution but also the wintering range of sika deer is likely to increase according to climate change (Fig. 3.7). An additional increase in wintering range can happen by cessation of management of evergreen plantation due to the snow interception by forest canopy (Minamino et al. 2007). Currently, sika deer become seasonally absent by migration in the areas with long snow cover duration, and the impact on vegetation becomes relatively insignificant (Ohashi et al. 2014, Fig. 3.5). However, as the area available for wintering expands, there are increasing concerns that the impact on vegetation will become more serious as deer become year-round inhabitants in the surroundings of the newly available wintering areas. The basis of biodiversity conservation in highly natural ecosystems is to maintain them in an "untouched" state without human development. However, such a traditional basis

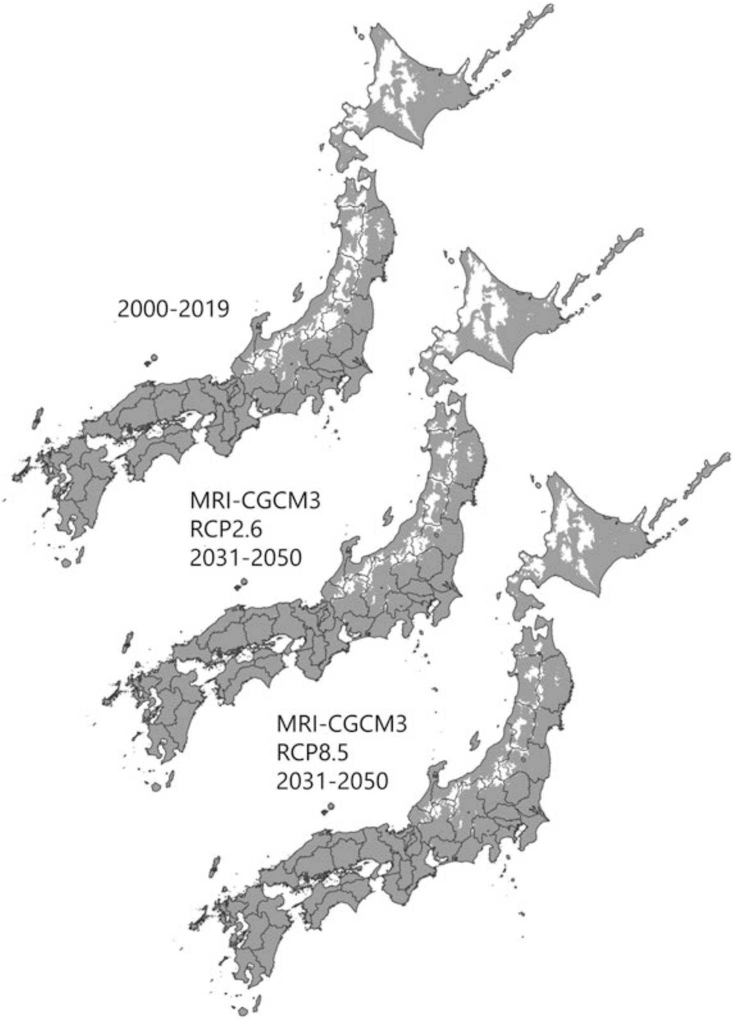

Fig. 3.7 Map of possible year-round habitat for deer in the present (2000–2019) and near future (2031–2050) based on snow condition. MRI-CGCM3 was used to calculate the future snow cover environment. Top, present (2000–2019); middle, 2031–2050 under the RCP2.6 scenario; bottom, 2031–2050 under the RCP8.5 scenario. Calculation was based on models in Ohashi et al. (2016) and bias-corrected climate scenario from Nishimori et al. (2019). The threshold of snow cover environment limiting the distribution of this species was set at 50 days or more with a snow depth of 50 cm or more in Honshu and 80 days or more with a snow depth of 60 cm or more in Hokkaido, referring to Tokida et al. (1980)

may not work for the current situation of sika deer management. It is urgent to establish a systematic deer management system in natural vegetation areas to maintain biodiversity in Japan, one of the world's biodiversity hot spots.

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Chapter 4
Estimation of Sika Deer Abundance by Harvest-Based Model and the Characteristics of Their Population Dynamics

Hayato Iijima

Abstract Although a harvest-based model (HBM) is a useful model to estimate wildlife abundance under hunting pressure and is wildly applied in the actual population management of sika deer (*Cervus nippon*) in Japan, the parameter-identifiable condition of HBM has rarely been clarified. In this study, I examined this condition in relation to the amount of direct abundance index, which is used to calculate absolute abundance from the data only and hunting pressure by data simulation. Furthermore, I applied HBM to the real monitoring data of sika deer that were collected in the Yamanashi Prefecture. Data simulation showed that the parameters of HBM were identifiable if the direct abundance index was available in 5% of the spatial units for abundance estimation, even if it was collected only in 1 year during the survey period. Furthermore, strong hunting pressure, which is comparable to population growth rate, increased the precision of parameter estimation. When HBM was applied to real data, sika deer abundance at 25.3 km^2 cells (5.5 km × 4.6 km) could be estimated without any informative prior distribution, and the median of intrinsic population growth rate was 0.146. In conclusion, HBM is a useful model to estimate wildlife abundance, but the estimable conditions should be carefully checked by scientific experts.

4.1 Introduction

The population of deer species in Canada (Côté et al. 2004), Britain (Putman and Moore 1998), and Japan (Iijima et al. 2013) has increased, considerably affecting vegetation (e.g., debarking [Akashi and Nakashizuka 1999; Iijima and Nagaike 2015], decrease in palatable plants [Iijima and Otsu 2018], and domination of

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H. Iijima (✉)
Department of Wildlife Biology, Forestry and Forest Products Research Institute, Tsukuba, Japan
e-mail: hayato.iijima@gmail.com

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unpalatable plants [Tanentzap et al. 2012]). In some cases, such effects remain for decades even if deer abundance is decreased or deer-proof fences are established (Royo et al. 2010; Nuttle et al. 2014; Otsu et al. 2019). Then, population management is of interest not only among biologists but also among managers. For a successful population management of deer species, estimation of their abundance must be estimated on the basis of the monitoring and determination of appropriate hunting and/or culling quota.

Various models for the abundance estimation of animals have been developed, and they can be characterized by population closure, individual distinguishability, target of estimation, and monitoring methods (Iijima 2020). The management of deer species continues for a long time, and the catching and marking of deer species are possible but time-consuming. Then, models for the open population of unmarked animals seem appropriate to estimate deer abundance. Open population distance sampling (Sollmann et al. 2015) and the open N-mixture model (Schmidt et al. 2015) can also be applied to estimate the abundance of the open population of unmarked animals. Researchers need to measure the distance and angle of found animals for distance sampling and to obtain replicated count data within a short time (i.e., closed population) for N-mixture model. Then, a careful experimental design and intensive survey effort are necessary to apply these models, although they might be difficult to prepare in actual population management.

Deer species are often game species in many countries (Solberg et al. 1999; Simard et al. 2013; Stout et al. 2013; Iijima 2017), and the number of hunted deer is well monitored. In addition to the number of hunted deer, relative abundance indices, such as sight per unit effort (SPUE; Uno et al. 2006), pellet group density (Rönnegård et al. 2008), and spotlight count (Garel et al. 2010; Uno et al. 2006), are usually monitored to evaluate the dynamics of them. A harvest-based model (HBM) estimates animal abundance under hunting pressure through the response of the abundance index to hunting pressure (Iijima 2020). HBM can be regarded as a hierarchical model (Royle and Dorazio 2008) that explicitly has a process model about animal population dynamics under hunting pressure and an observation model about the process of monitoring their abundance-by-abundance index. In the case of open populations, demographic parameters, such as intrinsic population growth rate, should be identified in addition to animal abundance. The use of other external data about demographic parameters is useful to improve the parameter identifiability of HBM. For example, Iijima et al. (2013) used the percentages of various landscape components, such as evergreen forests, in HBM to identify the intrinsic population growth rate of sika deer. Such HBM can be regarded as an integrated population model that estimates abundance and demographic parameters by incorporating various data about different components of demography (Schaub et al. 2007; Kéry and Schaub 2011; Schaub and Abadi 2011).

Although HBM has been applied to animal abundance estimation (Yamamura et al. 2008; Chee and Wintle 2010; Fukasawa et al. 2013; Iijima and Ueno 2016), the estimable condition of HBM has rarely been generalized. Fukasawa et al. (2020) showed that the usage of harvest quota as an abundance index caused a biased estimation of abundance. I expected that the type of abundance index was an important factor in determining the precision of population estimates. Iijima et al.

(2013) successfully estimated abundance and population growth rate without informative prior distribution using a direct abundance index. Direct means that an absolute density can be calculated by using only the observed abundance index. For example, deer density can be calculated as found deer by survey area of ground survey. Then, the simply derived density contains information about the order of true abundance, although it includes a measurement error. Furthermore, given that HBM tries to estimate abundance by the temporal change of abundance index under hunting pressure, I expected that the intensity of hunting is an important factor. If an abundance index annually increases at a constant rate, then estimating abundance and their population growth rate simultaneously is impossible.

The objective of this study is to show the applicability of HBM to the estimation of deer abundance under hunting pressure. To achieve the objective of this study, I conducted two specific studies: (1) a simulation study to examine the parameter-identifiable condition in HBM from the aspects of hunting intensity and availability of direct index and (2) an application study of HBM to actual monitoring data about sika deer.

4.2 Methods

My study has two parts as stated above. First, I examine the parameter identifiability of HBM, depending on the intensity of hunting pressure and the amount of available data by data simulation (Kéry and Royle 2015). Afterward, I apply HBM to real data about sika deer (*Cervus nippon*) in the Yamanashi Prefecture.

4.2.1 Simulation

The model structure of HBM is almost the same as the model of Iijima et al. (2013). I would like to estimate the sika deer abundance of discrete space and time. Assume the 10 × 10 grid cells and the sika deer abundance in each cell should be estimated. The size of each cell is 25.3 km^2, with a long side of 5.5 km and a short side of 4.6 km. The sika deer abundance of each cell decreases with hunting ratio, which is estimated from the relationship between the latent abundance and the number of hunted and culled deer, and increases with population growth rate. The survey period is 5 years. An indirect abundance index (IDI, e.g., SPUE) and a direct abundance index (e.g., the number of found deer by block count survey; Daniels 2006) are obtained. The IDI is obtained in 95% of spatial units (i.e., 100 cells) for all years, whereas the direct abundance index is obtained although the amount of data differs by scenarios (Table 4.1).

The process model of the HBM is as follows:

Table 4.1 The settings of hunting ratio and the availability of direct index in scenarios

Scenario	Hunting ratio	Availability of direct index	
		Spatial unit (%)	Year
0_1	0.03	0	
0_2	0.15	0	
1_1	0.03	2	The last 1 year
1_2	0.15	2	The last 1 year
1_3	0.03	5	The last 1 year
1_4	0.15	5	The last 1 year
2_1	0.03	2	The last 2 years
2_2	0.15	2	The last 2 years
2_3	0.03	5	The last 2 years
2_4	0.15	5	The last 2 years
3_1	0.03	2	The last 3 years
3_2	0.15	2	The last 3 years
3_3	0.03	5	The last 3 years
3_4	0.15	5	The last 3 years

$$x_{t,c} \sim \mathrm{N}\left(x_{t-1,c} + \log\left(1 - hr_{t-1,c}\right) + r_c, \sigma_1^2\right)$$

$$x_{1,c} \sim \mathrm{N}\left(xinit, \sigma_2^2\right)$$

$$xinit \sim \mathrm{N}\left(0, 10^4\right)$$

$$\mathrm{logit}(hr_{t,c}) \sim \mathrm{N}\left(yhr_t, \sigma_3^2\right)$$

$$yhr_t \sim \mathrm{N}\left(yhr_{t-1}, \sigma_4^2\right)$$

$$yhr_1 \sim \mathrm{N}\left(0, 10^4\right)$$

$$r_c \sim \mathrm{N}\left(\mu r, \sigma_5^2\right)$$

$$\mu r \sim \mathrm{N}\left(0, 10^4\right)$$

where $x_{t,c}$ is the sika deer abundance on the logarithmic scale in the cth cell of the tth year, $hr_{t,c}$ is the hunting ratio in the cth of the tth year, $xinit$ is the mean of sika deer abundance on the logarithmic scale in the first year (t=1), yhr_t is the yearly mean of hunting ratio in the tth year, r_c is the intrinsic population growth rate in the cth cell, and σs are the standard deviation of Gaussian distribution.

The observation model of the HBM about the IDI is as follows:

$$\mathrm{IDI}_{t,c} \sim \mathrm{Poisson}(\lambda\mathrm{IDI}_{t,c})$$

$$\lambda\mathrm{IDI}_{t,c} = \exp\left(\beta\mathrm{IDI} + x_{t,c} + \varepsilon\mathrm{IDI}_{t,c}\right)\mathrm{Effort}_{t,c}$$

Table 4.2 The parameter settings of data simulation

Parameter	Value	Parameter	Value
xinit	4.000	μr	0.182
σ_1	0.050	σ_2	0.500
σ_3	0.050	σ_4	0.200
σ_5	0.010	σ_6	1.000
σ_7	0.100	yhr_1	0.03 or 0.15

$$\beta\mathrm{IDI} \sim \mathrm{N}\left(0, 10^4\right)$$

$$\varepsilon\mathrm{IDI}_{t,c} \sim \mathrm{N}\left(0, \sigma_6^2\right)$$

where $\mathrm{IDI}_{t,c}$ is the observation value of the indirect index in the *c*th cell of the *t*th year, βIDI is the coefficient of indirect index that links the true abundance (i.e., $x_{t,c}$) and the observed value (i.e., $\mathrm{IDI}_{t,c}$), $\varepsilon\mathrm{IDI}_{t,c}$ is the random effect in the *c*th of the *t*th year, $\mathrm{Effort}_{t,c}$ is the effort to obtain the indirect index in the *c*th of the *t*th year, and σ_6 is the standard deviation of Gaussian distribution.

The observation model of HBM about the direct abundance index is as follows:

$$\mathrm{DI}_{t,c} \sim \mathrm{Poisson}(\lambda\mathrm{DI}_{t,c})$$

$$\lambda\mathrm{DI}_{t,c} = \exp\left(x_{t,c} + \varepsilon\mathrm{DI}_{t,c}\right)\mathrm{Effort}_{t,c}$$

$$\varepsilon\mathrm{DI}_{t,c} \sim \mathrm{N}\left(0, \sigma_7^2\right)$$

where $\mathrm{DI}_{t,c}$ is the observation value of the direct index in the *c*th cell of the *t*th year, $\varepsilon\mathrm{DI}_{t,c}$ is the random effect in the *c*th of the *t*th year, $\mathrm{Effort}_{t,c}$ is the effort to obtain the direct index in the *c*th of the *t*th year, and σ_7 is the standard deviation of Gaussian distribution.

The observation model of HBM about the hunting ratio is as follows:

$$\mathrm{C}_{t,c} \sim \mathrm{Binomial}(hr_{t,c}, D_{t,c})$$

where $\mathrm{C}_{t,c}$ is the number of hunted and culled deer in the *c*th cell of the *t*th year and $D_{t,c}$ is the sika deer abundance in the *c*th cell of the *t*th year (i.e., $D_{t,c} = \exp(x_{t,c})$). The prior distribution of all σs is vague uniform distribution as U(0, 100) (Gelman 2006).

Based on the above model, I generated the observation data (i.e., indirect index, direct index, and the number of hunted and culled deer with given parameters; Table 4.2). Then, I applied the HBM to the generated data and estimated the parameters of HBM by Markov chain Monte Carlo (MCMC) method.

4.2.2 Application of HBM to Real Data

I applied the above HBM to the real data that were obtained from the Yamanashi Prefecture in central Japan. In the Yamanashi Prefecture, the harvest quota of sika deer by game hunting and nuisance control, SPUE (indirect index), pellet group survey (indirect index), and block count survey (direct index) was monitored from 2005 in a square grid cell (ca. 25.3 km^2). Although the monitoring continues until now, I used the monitoring data from 2005 to 2018. SPUE was obtained in almost all cells in all years, the pellet group survey was obtained in ca. 40 cells in all years, and the block count survey was conducted in 10 cells during 2005 to 2014 (but 39 cells only in 2011). Although the total number of cells in the Yamanashi Prefecture is 216, I targeted 207 of 216 cells where SPUE was obtained at least 2 years during 2005 and 2018. The HBM for real data was similar to the model that was explained in data simulation. However, as stated above, the case of the Yamanashi Prefecture had two indirect indices. Then, two observation models about the IDI (i.e., SPUE and pellet group survey) were available. βSPUE and βPD corresponded to βIDI in the case of data simulation; σ_7 and σ_8 corresponded to the standard deviations of Gaussian distribution, which were prior distributions of the random effects of SPUE and the pellet group survey, respectively.

4.2.3 Parameter Estimation

The posterior parameter distributions of the above HBMs were estimated by MCMC method (Calder et al. 2003). MCMC was conducted by R (R Core Team 2020), JAGS (Plummer 2003), and *jagsUI* packages (https://github.com/kenkellner/jagsUI, accessed 2021/3/29). The number of MCMC chains was three. The initial burn-in of MCMC was 10 million iterations, and sampling after burn-in was 10 million iterations with a thinning interval of 1000 (i.e., 1000 samples were obtained per chain). I judged that the MCMC was converged if $\widehat{R}$ was lower than 1.1 (Gelman et al. 2004).

4.3 Results

4.3.1 Simulation

An example of generated data under the scenario 1_1 is shown in Fig. 4.1. In the scenario, the deer abundance of almost all cells annually increased because the mean population growth rate (0.2) was much higher than the mean of yearly hunting ratio (0.03). However, in the case of scenario 1_4 with high hunting ratio (0.15), deer abundance annually decreased (Fig. 4.2).

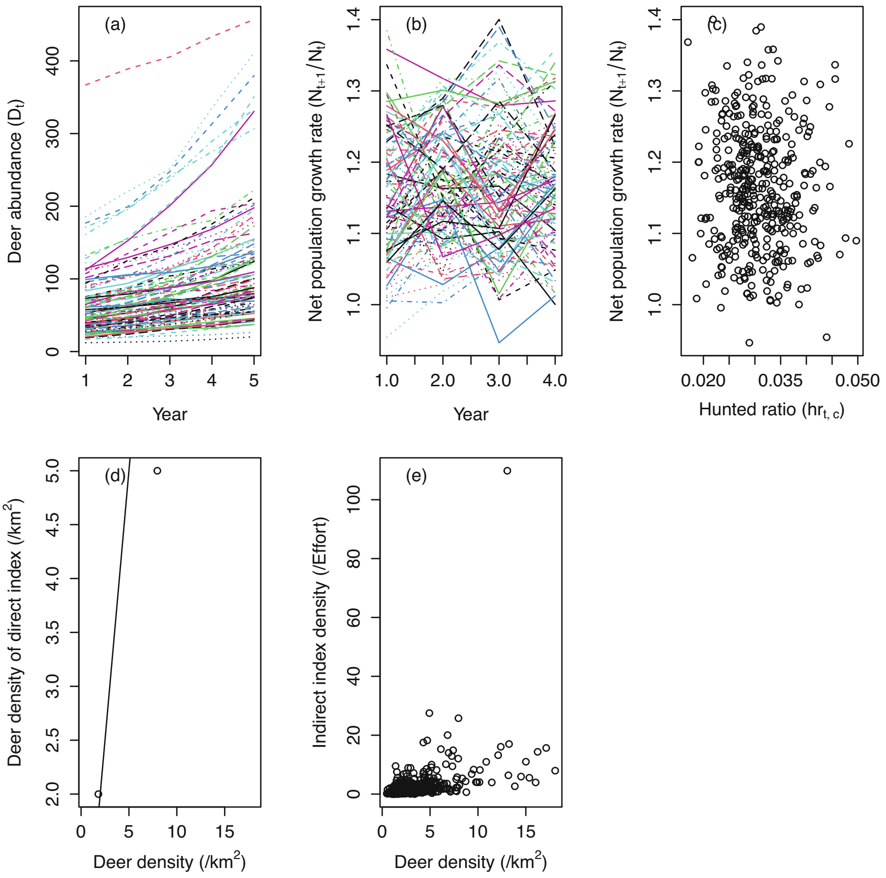

Fig. 4.1 Generated data under scenario 1_1. Note: In scenario 1_1, the hunting ratio was 0.03, and the direct abundance index was available in 2% of the grid cells, only in the last year of survey (Table 4.2). (**a**) Annual change of deer abundance in each cell. (**b**) Annual change of net population growth rate (N_{t+1}/N_t). (**c**) Relationship between hunting ratio and net population growth rate. (**d**) Relationship between latent deer density and deer density based on the direct abundance index. (**e**) Relationship between latent deer density and IDI density

When the direct index was not available or only 2% of spatial units were available, some model parameters did not converge (Fig. 4.3). Furthermore, the range of 95% credible interval of these estimates was large (Fig. 4.3). If direct index was available in 5% of the spatial units (i.e., scenarios 1_3, 1_4, 2_3, 2_4, 3_3, and 3_4), the posterior medians of abundance estimates were less biased than those of scenarios wherein a direct index was available in only 2% of spatial units.

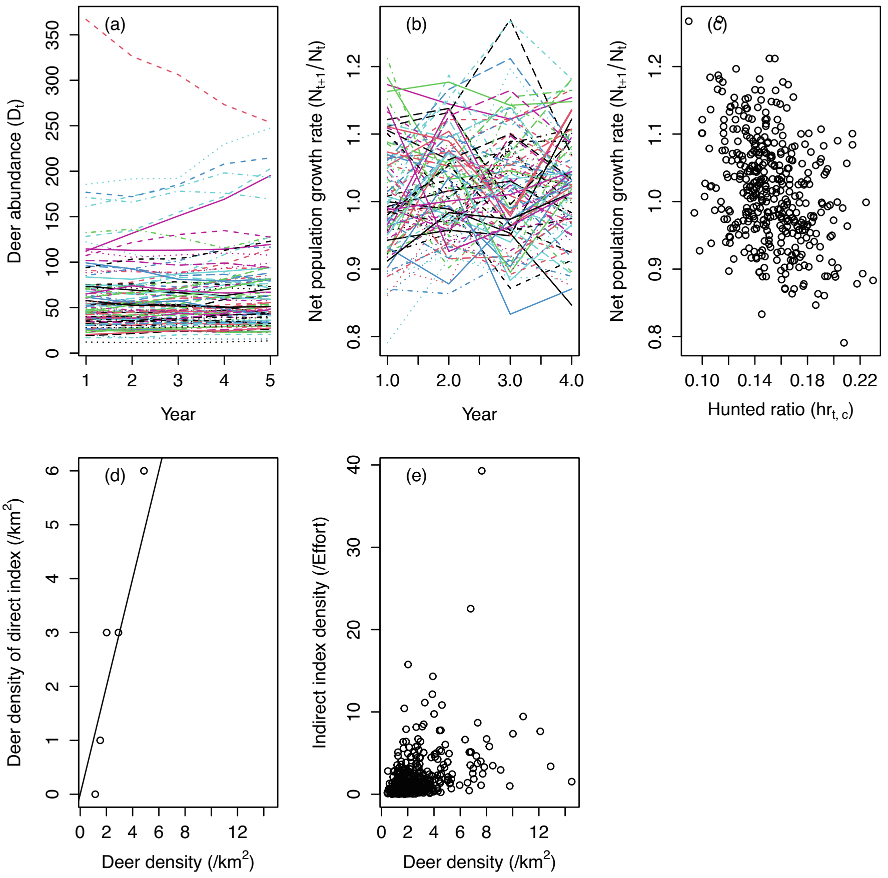

Fig. 4.2 Generated data under scenario 1_4. Note: In scenario 1_4, the hunting ratio was 0.15, and the direct abundance index was available in 5% of the grid cells, only in the last year of survey (Table 4.2). (**a**) Annual change of deer abundance in each cell. (**b**) Annual change of net population growth rate (N_{t+1}/N_t). (**c**) Relationship between hunting ratio and net population growth rate. (**d**) Relationship between the latent deer density and the deer density based on the direct abundance index. (**e**) Relationship between the latent deer density and IDI density

4.3.2 Real Data

All parameters of the model were converged. Although I used vague prior distributions for parameters, the posterior distributions had an evident and single peak of probability density (Fig. 4.4). The estimated abundance generally correlated with SPUE, pellet group density, and block count survey (Fig. 4.5). The temporal trends of the estimated abundance of cells varied among cells, but abundances in many cells tended to decrease from 2012. The posterior median of the highest sika deer density in a cell was 78.7 (/km^2). The posterior median of the sika deer density of the Yamanashi Prefecture annually increased from 7.9 (/km^2) in 2005 to 14.3 (/km^2) in

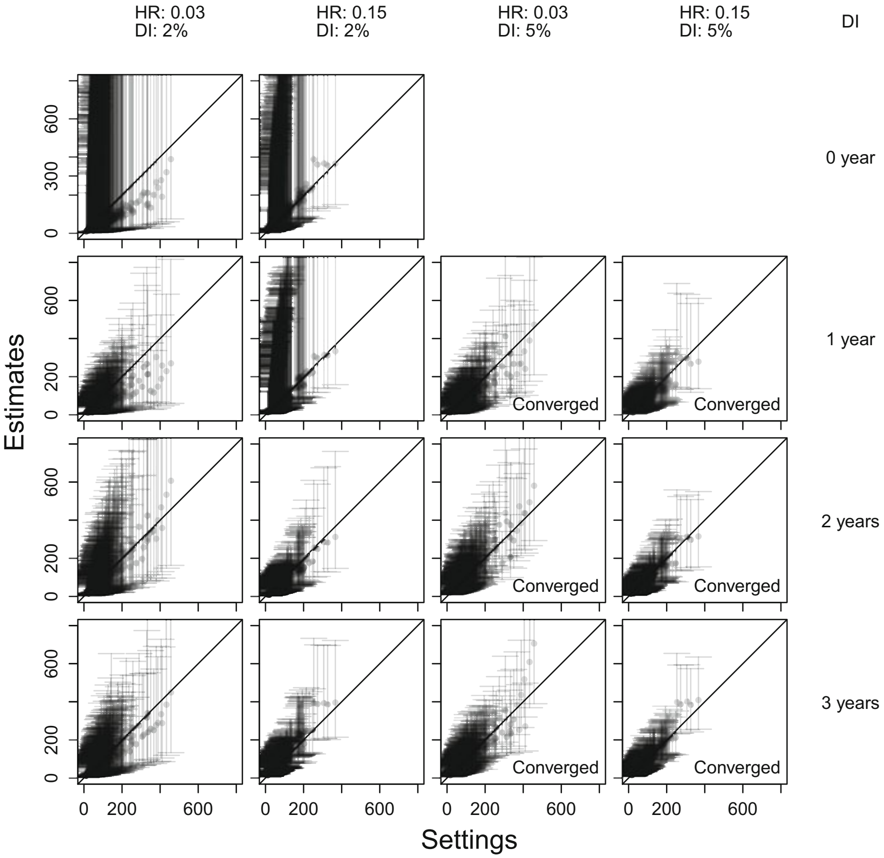

Fig. 4.3 True (set) and estimated deer abundance under various scenarios. Note: Circles and error bars indicate the median and 95% credible intervals of posterior distribution. HR, mean hunting ratio; DI, direct index

2013 but decreased to 11.4 (/km^2) in 2018. The posterior median of intrinsic population growth rate was 0.146 (0.121 to 0.171; 95% credible interval), and the derived population growth rate was 1.157 (1.129 to 1.187; 95% credible interval). The mean of the estimated hunting ratios of all cells in 2005 was 0.03. However, it annually increased and reached 0.137 in 2012 and 0.192 in 2017 (Fig. 4.6). A higher hunting ratio suppressed the population growth of sika deer (Fig. 4.7).

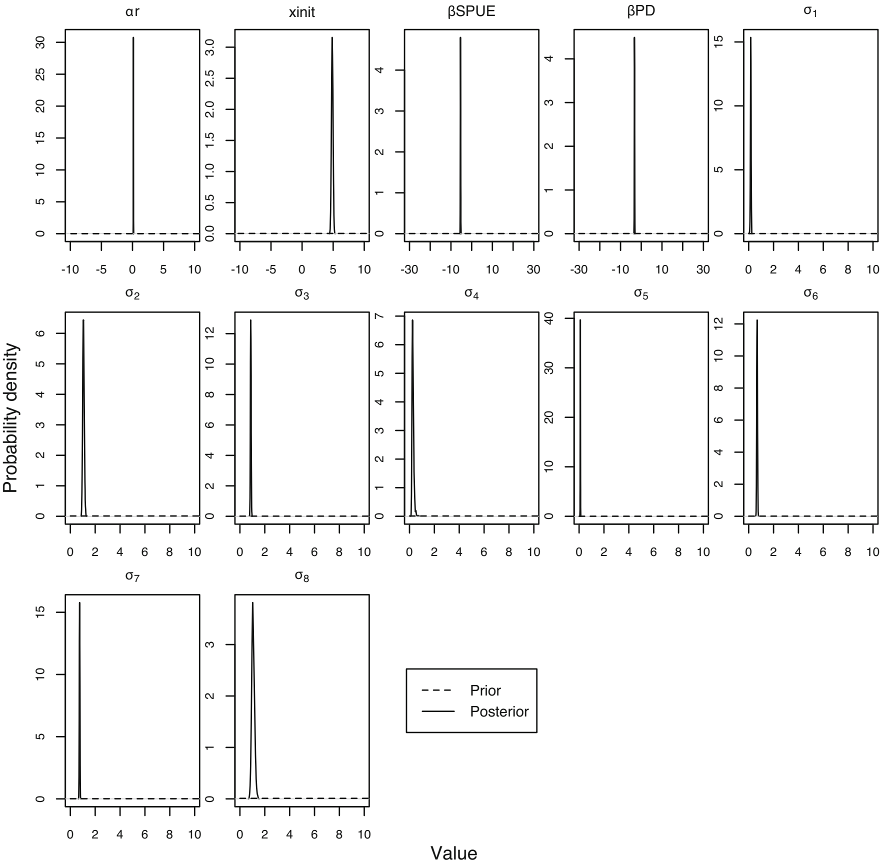

Fig. 4.4 Relationship between prior and posterior distributions

4.4 Discussion

4.4.1 Parameter-Identifiable Conditions of HBM

Data simulation showed that the parameter identifiability of HBM was greatly affected by the amount of available direct index and hunting ratio. Without a direct index, MCMC did not converge (Fig. 4.3). Because there are many possible combinations of abundance and population growth rate to express the annual change of abundance index, the existence of a direct index that gives the information of the order of abundance is crucial for the parameter identifiability of HBM. However, obtaining a direct index in all target spatial units is unrealistic in actual management situations. Therefore, the required amount of direct index for a successful estimation of deer abundance by HBM should be clarified.

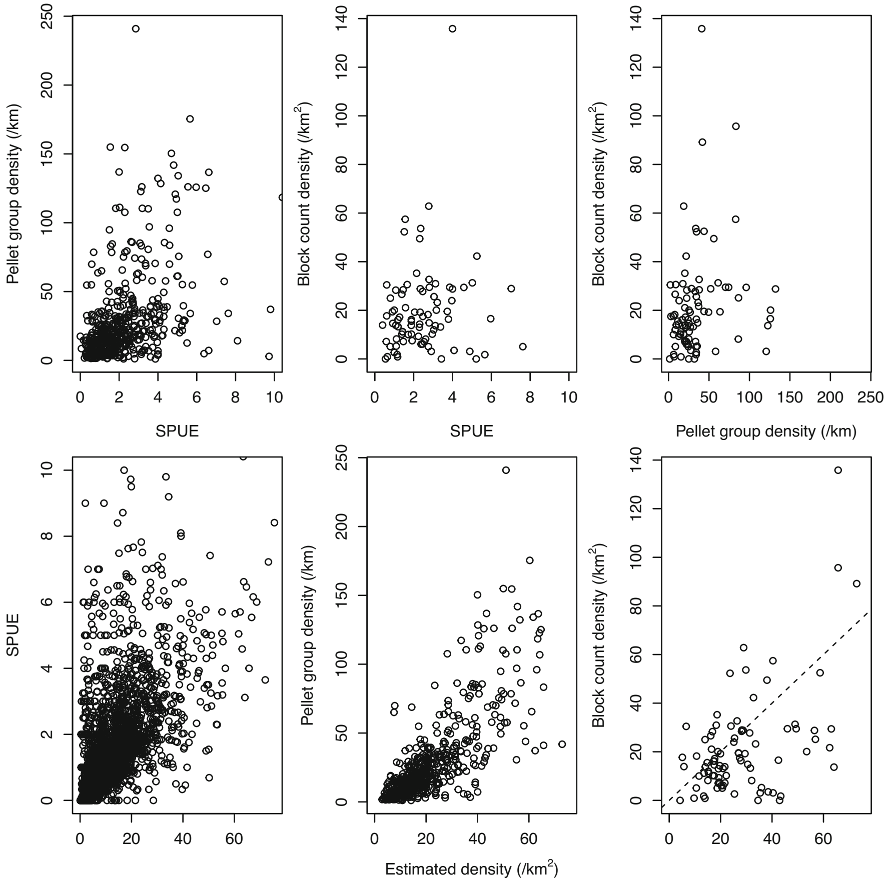

Fig. 4.5 Relationship between data and estimated deer abundance

Data simulation showed that the direct index should be collected from 5% of the spatial units. In real data, the block count survey was used as direct abundance index, and it was obtained in 4.8% of the spatial units (10/207). Furthermore, all parameters converged, and the peaks of their probability density could be identified from vague priors (Fig. 4.4). However, the measurement error of block count is empirically known as large. Then, the measurement error should be considered in an observation model. I considered the large observation error by using log-normal random effect. The survey for the abundance estimation of closed population can be an alternative of the direct index. Given that HBM is a type of integrated population model, the collected data for the abundance estimation of closed population can be linked to the latent abundance with an appropriate observation model. If the direct index or data for the abundance estimation of closed populations is not available, then setting of the initial abundance based on the reliable information can be an alternative (Fukasawa et al. 2013).

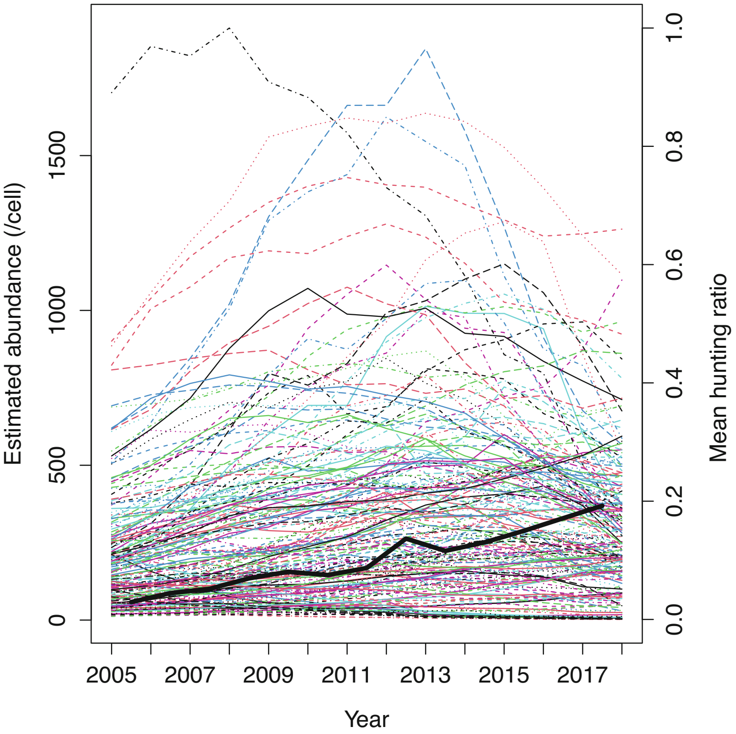

Fig. 4.6 Estimated abundance dynamics of the Yamanashi Prefecture. Note: Bold black and other lines indicate the mean hunting ratio of the *t*th year (yhr_t) and the estimated abundance of each cell, respectively

Hunting ratio was also suggested to be an important factor for the parameter identifiability of HBM. The range of 95% credible interval of parameters of the model with high hunting ratio tended to be narrower than that of the model with low hunting ratio (Fig. 4.3). The decrease in abundance index is important information for abundance estimation because such decrease indicates the order of abundance. Although I could not show the threshold of hunting ratio for a successful abundance estimation by HBM, a high hunting ratio corresponding to population growth rate is necessary for a successful abundance estimation by HBM.

4.4.2 Characteristics of Sika Deer Population Dynamics

The median of the intrinsic population growth rate of sika deer in the Yamanashi Prefecture (0.146) was similar to that of sika deer in Nakanoshima Island (0.157; Kaji et al. 2004) in the northern part of Japan but was lower than that of sika deer in the Yamanashi Prefecture during 2005 and 2010 (0.253; Iijima et al. 2013). Given

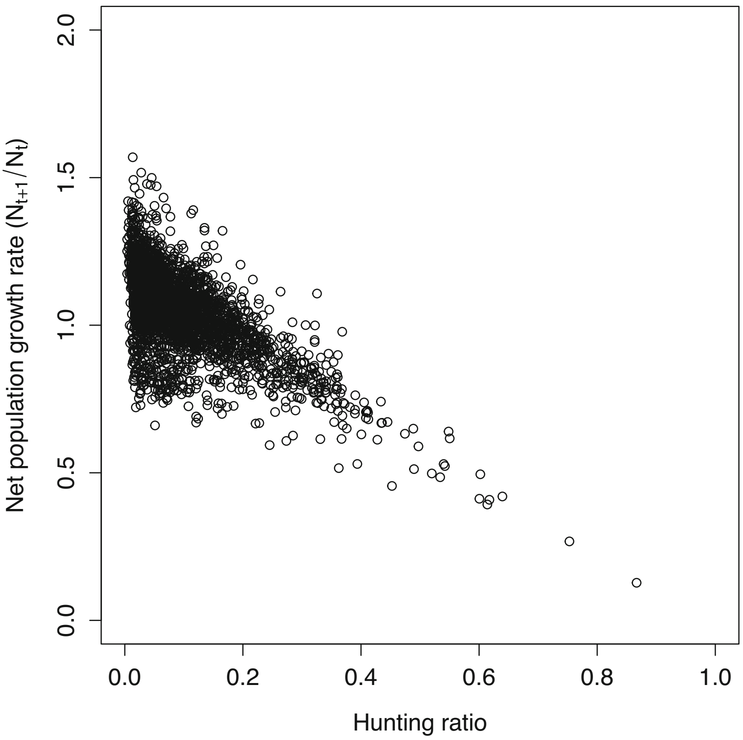

Fig. 4.7 Relationship between hunting ratio and net population growth rate

that the hunting ratio was low during 2005 and 2010, the sika deer population annually increased in many places in the Yamanashi Prefecture at that time (Fig. 4.6). By contrast, the data of our study and that of Kaji et al. (2004) included the decrease or plateau of sika deer abundance by strong hunting ratio or density dependence. Therefore, the difference may be caused by the phase of sika deer population expansion. These estimated intrinsic population growth rates were below the theoretically maximum population growth rate of sika deer (0.38; Hone et al. 2010 and 0.31; Matsuda et al. 1999). Therefore, the estimate of the intrinsic population growth rate of this study is valid.

4.4.3 Implications for Actual Population Management

In most prefectures in Japan, the abundance of sika deer is a major objective of sika deer management, and HBM is adopted as the most popular model to estimate their abundance (Iijima 2018). However, the scientific validity of such HBMs has rarely been examined (Iijima 2018). For example, a HBM that was compliant with a HBM of the Ministry of Environment, Japan, used the number of hunted deer as an IDI without considering hunting effort and used the averaged monitoring data (originally collected in spatially fine scale) by the prefecture unit (Iijima 2018). About the former issue, the usage of the number of hunted deer as an IDI in HBM was proven to be the cause of the biased estimation of latent abundance (Fukasawa et al. 2020). About the latter issue, the aggregation of data into a spatially large scale overlooks the effect of hunting pressure on abundance indices. As discussed above, the decreasing trend in abundance indices is important for the parameter identifiability of HBM. Furthermore, the spatial difference of abundance and hunting ratio was important information for actual population management. Spatial heterogeneity was observed in sika deer abundance and hunting ratio (Fig. 4.6), and setting a priority of hunting effort or a budget for nuisance control in a spatially fine scale was probably effective for population management. For this reason, the spatial units for monitoring and abundance estimation should be matched, and the monitoring data should not be averaged in spatially broad unit. The example indicates that the usage of HBM in the abundance estimation of sika deer is not a simple and an easy task, and a careful scientific evaluation of HBM by scientific experts must be conducted. Some conditions for the parameter identifiability in HBM were clarified in this study and thus contribute to the scientific evaluation of HBM in actual population management.

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Chapter 5
Variation in the Local Sika Deer Density between Three Areas of Japan with Diverse Climatic Conditions

Mayumi Ueno, Hayato Iijima, Masahiko Asada, and Daiki Watanabe

Abstract Sika deer are distributed throughout habitats with various landscape compositions under different climate conditions, although the spatial differences in their population demographics and related factors have rarely been examined. First, we estimated the density and growth rate of sika deer in three areas of Japan with diverse climatic conditions (Kushiro in Hokkaido, Yamanashi, and Boso in Chiba) by the fine-spatial-scale (local) and derived global density for each area. Second, we examined the effects of environmental variables on the spatial variations in the local density and finite rate of natural increase. The global density for Kushiro exceeded 20 deer/km^2 during 2005–2012, while those of the other areas (Yamanashi and Boso) were below 20 deer/km^2. However, the extent of local density overlapped between Kushiro, Yamanashi, and Boso, ranging from 3 to 36 deer/km^2. Positive influential factors for the local density included the proportions of deciduous broad-leaved forests, mixed forests, artificial meadows, and the annual mean temperature, while the total proportion of residential area was a negative factor. Thus, a high density of up to 40 deer/km^2 in any area of Japan appears locally possible, regardless of the climate conditions. The finite rate of population increase was estimated to range from 0.9 to 1.7, which covers the range of potential sika deer population growth rates. Therefore, the target density to effectively manage and predict sika

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M. Ueno (✉)
Research Institute of Energy, Environment and Geology, Hokkaido Research Organization, Sapporo, Japan
e-mail: ueno-mayumi@hro.or.jp

H. Iijima
Department of Wildlife Biology, Forestry and Forest Products Research Institute, Tsukuba, Japan
e-mail: hayato.iijima@gmail.com

M. Asada
AMAC LLC, Sakura, Japan
e-mail: asada.amac@gmail.com

D. Watanabe
Research Faculty of Agriculture, Hokkaido University, Sapporo, Japan
e-mail: mixjuice337@yahoo.co.jp

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deer populations should be based on a local scale. Database by 5 km square grid cells applied for sport hunting in Japan would be useful and should be expanded to other prefectures and database for nuisance control.

5.1 Introduction

Quantifying the spatial distribution of the abundance of a species is important for ecology, biogeography, conservation, and management (Brown et al. 1995). Environmental factors play key roles in determining the spatial patterns of the abundance of individual species (Mysterud et al. 2002; Maier et al. 2005; Morellet et al. 2011). However, a large number of datasets providing estimates of the local density, along with underlying environmental data, are required to characterize favorable habitats for globally distributed species.

Many methods to determine population abundance at the local scale under static conditions (i.e. closed-population, Iijima 2020), such as capture-mark-recapture methods (Williams et al. 2002), distance sampling (Thomas et al. 2010), random encounter modeling (Rowcliffe et al. 2008), and random encounter and staying time modeling (Nakashima et al. 2018), have been developed. However, these methods require intensive research and may be too expensive to operate regularly; therefore, they are rarely applicable at larger scales (Ueno et al. 2014). Furthermore, in recent years, the abundance of some wildlife species has increased, causing human–wildlife conflict. Therefore, a model to estimate the abundance of wildlife in an open population by considering the effect of population control is necessary.

Recently, harvest-based modeling has been used to estimate the population dynamics of wildlife under population control (Yamamura et al. 2008; Asada et al. 2014; Fukasawa et al. 2013; Iijima et al. 2013; Iijima and Ueno 2016; Osada et al. 2015; Takeshita et al. 2017). As the harvest-based model treats the number of hunted and/or culled wildlife as a population dynamics process, it may be suitable for estimating the abundance of wildlife under population control (Chap. 4). Furthermore, the harvest-based model can be extended as a hierarchical model (Royle and Dorazio 2008) to separate the unobserved state process from the observation process, which includes various sources of uncertainty in field observations. Additionally, multiple abundance indices can be integrated into an observational model. The number of hunted individuals is recorded for game species, and some abundance indices, such as hunting statistics, are usually monitored at a broad scale for many years to aid in management. However, such observations are sometimes missing. A hierarchical model can treat such missing values by describing the latent state of wildlife abundance within all target spatial and temporal units in the process model and considering the observation process of such incomplete data in the observation model. Therefore, harvest-based modeling based on the number of hunted wildlife and abundance indices is feasible for regular wildlife monitoring.

The distribution of sika deer (*Cervus nippon*) in Japan is either continuous or sometimes localized, indicating the involvement of environmental factors (Biodiversity Center of Japan, Nature Conservation Bureau, Ministry of the Environment

2010). However, the differences in their densities between areas and their affecting factors have rarely been examined. Understanding the spatial structure of the population density of sika deer in relation to the environment will aid their conservation and management.

This study aimed to evaluate the spatial variation in the density and growth of sika deer inhabiting Japan. Based on the three populations with different climate conditions (Kushiro, Boso, and Yamanashi), we first compared the population density and finite rate of natural increase within and between areas. We then examined the environmental variables (obtained from meteorological stations) and population densities affecting the spatial variations in the local density and finite rate of natural increase in sika deer. Finally, we stated the importance of estimating local densities for managing sika deer populations.

5.2 Methods

5.2.1 Study Area

For comparison, we selected three areas representing the variability of the climatic conditions of Japan, which may affect the spatial heterogeneity of the population abundance and its growth rate (Fig. 5.1). The three areas were Kushiro (5997 km^2) in Hokkaido Prefecture, all areas of Yamanashi Prefecture (4465 km^2), and the Boso area (837 km^2) of Chiba Prefecture. The distribution pattern of vegetation in the Japanese archipelago, which has mountain ranges exceeding 3000 m, is characterized by horizontal variations with latitude and vertical variations with altitude. When comparing climate conditions between the three areas, Kushiro, located at the highest latitude, experiences warm summers and very cold winters with heavy snow (Table 5.1). However, Yamanashi and Boso, located at moderate latitudes, experience warmer and more humid summers and milder winters. Additionally, owing to the effect of altitude, Yamanashi experiences cold winters with very heavy snow in mountainous areas (Table 5.1). Furthermore, there are spatial differences in temperature and precipitation within these areas. Hence, the diverse climatic conditions of the three areas might affect the spatial heterogeneity in the population abundance and growth of sika deer throughout the feeding environments in Japan (Takatsuki 2009). In fact, according to an analysis of rumen contents, sika deer in the Boso area browsed evergreen woody species all year round, whereas sika deer in a neighboring area of Kushiro grazed agricultural pasture, which reflects surrounding landscape elements (Yokoyama et al. 2000; Asada and Ochiai 2009).

Kushiro is Kushiro-subprefecture located in the eastern area of Hokkaido. For Kushiro, forest covers 62% of the land. Natural forests include deciduous broad-leaved forest (23%) (*Acer mono*, *Tilia japonica*, *Quercus crispula*) and mixed forest (12%) with evergreen conifer trees (*Abies sachalinensis*, *Picea jezoensis*). Major tree species in the artificial forests (15%) are *A. sachalinensis* and *Larix kaempferi*. Flatland consists of artificial meadow (16%) and natural grassland that includes

Fig. 5.1 Three study areas of Japan (A: Kushiro in Hokkaido, B: Yamanashi, and C: Boso in Chiba)

marshland (5%) and bamboo grasses (2%). The remainder is residential area (1%), agricultural cropland (1%), and others (12%). For Yamanashi, forest covers 75% of the land. Natural forests include deciduous broad-leaved forest (31%) and evergreen forest trees (11%). Major tree species are *Acer*, *Betula*, and *Quercus spp.*, *Abies*, *Picea*, and *Tsuga spp*. Artificial forest accounts for 28%, and their major tree species are *Chamaecyparis obtusa*, *Larix kaempferi*, *Cryptomeria japonica*, *Pinus densiflora*. Flatland consists of artificial meadow (1%) and natural grassland (6%). The remainder is residential area (3%), agricultural cropland (11%), and others (3%). Boso is located in Boso Peninsula, Chiba prefecture. For Boso, forest covers 45% of the land, consisting of deciduous (15%) and evergreen (10%) broad-leaved forests and artificial evergreen forests (18%). Major tree species are *Quercus serrata*, *Machilus thunbergii*, *Castanopsis cuspidate* var. *sieboldii* and planted *Lithocarpus edulis*, natural coniferous forests of *Abies firma* and *Tsuga sieboldii* and *Chamaecyparis obtuse*. Flatland consists of artificial meadow (5%) and natural grassland (1%) and bamboo grasses (1%). The remainder is residential area (11%), agricultural cropland (32%), and others (4%).

Table 5.1 Backgrounds and summary of data for the three study areas. *Mean body mass for adult females was cited from Kubo and Takatsuki (2015)

Area name (prefecture)	Kushiro (Hokkaido)	Yamanashi (Yamanashi)	Boso (Chiba)
Data summary			
Data period	1994–2016	2005–2018	2000–2012
Area size (km^2)	5997	4465	837
Spatial scale for an estimation mesh unit	5 km square grid cell (23 km^2)	5 km square grid cell (25.3 km^2)	Original unit ranging from 1.2 to 34.6 km^2
Number of units	257 cells	212 cells	78 units
Background			
Annual precipitation (mm)	1112(866–1255)	1571(1051–3069)	1973(1568–2146)
Annual temperature (°C)	5(2–6)	10(1–14)	15(14–15)
Maximum of snow depth (cm)	65(31–116)	25(6–44)	4(2–5)
Coverage of DBL forest	0.3(0.0–0.91)	0.4(0.0–0.91)	0.3(0.1–0.84)
Coverage of EBL forest	0.1(0.0–0.85)	0.3(0.0–0.79)	0.3(0.0–0.60)
Mean body mass of females (kg)	84	52	40
Mean density (deer km^2) and its reference	28 (3–81) This study	8(0–67) Iijima et al. (2013) and this study	21(1–36) Asada et al. (2014)

The sika deer distributed in the three areas of Japan share the same genetic background (Nagata et al. 1998; Nagata 2009); however, their body mass exhibits large spatial variations (Kubo and Takatsuki 2015).

5.2.2 *Population Abundance Data and Estimation Procedure*

The population abundance data we used for comparison had different origins. The abundance for Kushiro was originally estimated in this study, while that for Yamanashi was re-estimated by adding data for new period following a procedure described in a previous study (Iijima et al. 2013). The abundance in Boso was also obtained from a previous study (Asada 2014; Asada et al. 2014). Following this paragraph, we describe how we estimated the population of Kushiro, while the population estimation processes for Yamanashi and Boso are only summarized. Further details regarding the data for Yamanashi and Boso are provided in the original articles. The overall comparable information is presented in Table 5.1.

5.2.2.1 Kushiro

We estimated the population abundance at a scale of approximately 5 km square grid cell (5.0 km $\times$ 4.6 km $=$ 23.0 km^2 for Kushiro; hereafter, mesh unit) during 1994–2016. The data used included the (1) number of hunted and culled deer, (2) number of sightings of sika deer per unit effort (SPUE) based on hunters' reports, (3) number of deer counted by a spotlight survey during 1994–2016, and (4) number of deer by counted distance sampling in 2013 and 2014 (Uno et al. 2017). These data were obtained in mesh units for each year. A total of 257 mesh units were targeted, in which hunting and nuisance control have been conducted for over five years, and at least one was animal sighted in the latest year (2016). The hunting season was previously the end of January but was extended to February after 2004 and March after 2009. However, as the SPUE increased significantly in winter (Biodiversity Center of Japan, Nature Conservation Bureau, Ministry of the Environment 2008), we used the SPUE values from October to November. We fitted the hierarchical model for these data as follows:

—*Process model.*

The deer population dynamics in our harvest-based model for the Kushiro area can be expressed as follows:

$$D_{t,m} = D_{t-1,m}(1 - FHC_{t-1,m})r_m$$

where $D_{t,m}$ is the deer abundance in year t (1994, 1995, . . ., 2016) and mesh unit m ($m = 1, 2, \ldots, 257$), $FHC_{t\text{-}1,m}$ is deer hunting and culling rate for year t-1 in mesh unit m, and r_m is the mean population growth rate in mesh unit m for each year during the research period. Therefore, we assumed that the deer population increased annually at a constant rate during the study period and was decreased by hunting and culling, the effect of which differed each year.

If $\log(D_{t,m}) = x_{t,m}$ and $\log(r_m) = r_{log;m}$, then the process follows a linear structure. Eq. (1) can then be rewritten as follows:

$$x_{t,m} = x_{t-1,m} + \log\left(1 - FHC_{t-1,m}\right) + r_{log\,;m}$$

We introduced stochasticity to the deer population dynamics as follows:

$$x_{1,m}\tilde{\mathrm{N}}\left(xinit, \sigma_x^2\right)$$

$$xinit\tilde{\mathrm{N}}\left(0.0, 10^3\right)$$

We assigned a uniform prior for $\sigma\sim(0, 10^2)$ (Gelman 2006).

—*Observation model.*

We then developed three observation models for the relationship between the number of individuals and the number of observations using (1) SPUE, (2) spotlight count (SC), and (3) distance sampling. The characteristics of each survey are explained in Uno et al. (2006, 2017).

The observation model of SPUE is as follows:

$$S_{t,m} \sim \text{Poisson}(\lambda_{SD;\,t,m})$$

$$\lambda_{SD;\,t,m} = \exp\left(b_{SD} + x_{t,m} + \varepsilon_{SD;\,t,m}\right) \times E_{t,m}$$

where $S_{t,m}$ and $E_{t,m}$ are the number of sightings and effort (i.e. number of hunting days multiplied by the number of hunters) for year t in mesh unit m, respectively. b_{SD} is the coefficient linking the log deer abundance (i.e. $x_{t,m}$) to the sightings (i.e. $S_{t,m}$), and $\varepsilon_{SD;t,m}$ is a random effect.

The observation model regarding the spotlight count is as follows:

$$SC_{t,m} \sim \text{Poisson}(\lambda_{SC;\,t,m})$$

$$\lambda_{SC;\,t,m} = \exp\left(b_{SC} + x_{t,m} + \varepsilon_{SC;\,t,m}\right) \times L_{t,m}$$

where $SC_{t,m}$ and $L_{t,m}$ are the number of observations and length of the route (km) of the spotlight count survey for year t in mesh unit m, respectively.

The observation model for distance sampling is as follows (see Chap. 8 in Kéry and Royle 2015):

$$\text{DS}_{t,m} \sim \text{Multinomial}\left(D'_{t,m}, \pi_h\right)$$

$$D'_{t,m} = D_{t,m} \times \frac{\text{L}_{t,m} \times \text{B} \times 2}{\text{A}}$$

$$\pi_h = \frac{1}{\text{H}} \int_{b_{h-1}}^{b_h} \Pr(y = 1 | x, x \in h) dx$$

$$g(x;\sigma) = \exp\left(-x^2/2\sigma^2\right)$$

where $\text{DS}_{t,m}$ is the vector of the number of observed sika deer by distance sampling for year t and mesh unit m of each distance category h, $\text{L}_{t,m}$ is the route length of distance sampling for year t and mesh unit m, B is the maximum distance to which individuals are counted, A is the mesh unit area, H is the number of distance categories (15; 0–20, 20–40, ..., 280–300 m), $g(x)$ is the detection function (half-normal function), x is the perpendicular distance between the census route and observed deer, and σ is the scale parameter of $g(x)$. In distance sampling, the perpendicular distance was recorded at 10-m intervals from the census route. However, we binned these data into 20-m intervals to stabilize the estimation.

We estimated the parameters of the above model following the Markov chain Monte Carlo (MCMC) method using R (R Core Team 2020) and JAGs (Plummer 2003), which generates a stationary target distribution and converges it by constructing a Markov chain. The posterior distribution of the estimated parameters was determined using a Gibbs sampler. The first 200,000 samples were discarded, and every 200 samples were sampled 1000 times. We determined a parameter to be converged if $\widehat{R} < 1.1$ (Gelman et al. 2004).

5.2.2.2 Yamanashi

Population abundance data were estimated at a scale of approximately 5 km square grid cell (5.5 km × 4.6 km = 25.3 km^2 for Yamanashi; hereafter mesh unit) during 2005–2018. The population abundance was estimated based on harvest data, fecal pellet counts, SPUE, and block-count surveys from 2005 to 2018 in 212 mesh units (Table 5.1). The population estimation procedure was based on that of Iijima et al. (2013). Owing to the increased annual length of available data since Iijima et al. (2013), we re-estimated the population abundance following the same procedure.

5.2.2.3 Boso

Population abundance data were estimated by the scale of the prefecture's original management unit during 2000–2012. As a total of 78 units were constructed considering administrative borderlines, their sizes ranged between 1.2 and 34.6 km^2 (Asada 2014; Asada et al. 2014). The population abundance was estimated based on harvest data, fecal pellet counts, and block-count surveys conducted from 2000 to 2012. The population estimation procedures are described in Asada et al. (2014) and Asada et al. (2014).

5.2.3 Comparison between Areas

To conduct inter-regional analysis, we divided the posterior median of abundance ($D_{t,m}$) by the unit size (km^2) within areas to obtain the density. We defined the unit-based density as "local density" and the mean value of those local densities within areas as the "global density." Additionally, the study period for estimation differed between the areas. Data from 2005 to 2012 covering all areas were used to determine the annual mean.

First, we modeled the effects of different factors on the spatial variations in the local density by fitting generalized linear models assuming that the local density followed a Gaussian distribution. The explanatory variables for the density model included "region" (Kushiro, Yamanashi, Boso) as a categorical factor and several numerical factors related to landscape elements and climate conditions. Specifically, we considered the following landscape elements: (1) natural grassland, (2) deciduous broad-leaved forest (DBL), (3) evergreen forest, (4) mixed forest, (5) other forests, (6) artificial meadow, (7) agricultural facilities, (8) residential area, and (9) others occupying the area. The climate conditions included the annual (1) mean temperature (°C), (2) mean precipitation (mm), and (3) deepest snow depth (cm) during December and March based on statistics for the latest 30 years. The landscape elements and climate conditions were based on vegetation surveys (1/50,000) by prefecture cited from the Biodiversity Center of Japan, Ministry of the Environment (http://gis.biodic.go.jp/webgis/sc-025.html?kind=vg). The climatic conditions were obtained from the National Land Information Division, National Spatial Planning, Regional Policy Bureau, Ministry of Land, Infrastructure, Transport and Tourism of Japan (https://nlftp.mlit.go.jp/ksj/gml/datalist/KsjTmplt-G02.html). We preliminarily omitted one of the two variables that were strongly correlated (correlation coefficient > 0.6). When we modeled the effects of these factors on the spatial variations in the rate of natural increase in the sika deer populations, we used the variables discussed above and "population density" as an internal factor of density dependence. The best model was selected using AIC (Akaike's Information Criterion) in backward selection. We also compared the unit-based landscape variables selected by the best model between Kushiro, Yamanashi, and Boso.

5.3 Results

5.3.1 Differences in Global Density between the Three Areas

The Sika deer population of Kushiro exhibited two peaks in density during 1994–2016 (Fig. 5.2A). The first peak occurred in 1998, at 31 deer/km^2, and the

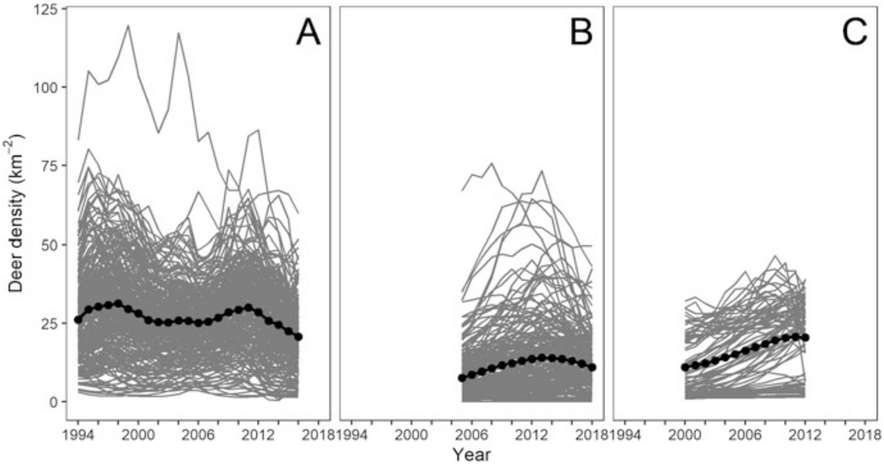

Fig. 5.2 Annual changes in the local and global density of sika deer in the three areas of Japan. Gray and black lines indicate the local and global density of sika deer, respectively. A: Kushiro, B: Yamanashi, C: Boso. Global density was the annual mean of the local densities within the areas

second occurred in 2012, at 30 deer/km^2. For Yamanashi, the sika deer population increased in abundance from 2005 to 2013, peaking at 14 deer/km^2, and stabilized thereafter (Fig. 5.2B). The population of Boso increased in number from 2000 to 2012, peaking at 14 deer/km^2, and then stabilized during the last few years (Fig. 5.2C). The global density for Kushiro during 2005–2012 was significantly higher than those for Yamanashi and Boso and did not overlap during any year of the period; the lowest estimated global density for Kushiro (20 deer/km^2) was equivalent to the highest estimated global density for Yamanashi and Boso (Fig. 5.2).

The scattering time series for local density indicates that the local densities within areas were not synchronized with the annual global density.

5.3.2 Large Variation in Local Density

The local density values varied between all three areas (Fig. 5.3). The annual mean local density during 2005–2012 for Kushiro ranged from 3 to 81 deer/km^2, with a median of 28 deer/km^2 (Fig. 5.3A), and the density in Kushiro was highest among the three areas. The annual mean local density for Yamanashi during 2005–2012 ranged from 0 to 67 deer/km^2, with a median of 8 deer/km^2(Fig. 5.3B). The annual mean local density for Boso ranged from 1 to 36 deer/km^2, with a median of 21 deer/km^2 (Fig. 5.3C). Therefore, the range of the local density overlapped between the three areas by 0–36 deer/km^2. The distribution of the local density exhibited two peaks for Boso (Fig. 5.3C).

The annual mean local density is shown on the map in Fig. 5.4, and local density was spatially structured. Several clusters of high-density units were observed in Kushiro, Yamanashi, and Boso (Fig. 5.4). For Boso, high-density units were clustered in the center, while low-density units were clustered in the periphery (Fig. 5.4C).

The landscape model for local density with the lowest AIC value included the proportions of (1) DBL, (2) mixed forest, (3) artificial meadow, (4) residential area, (5) annual mean temperature, and (6) area (Table 5.2), and its intercept indicated the mean local density in Boso. The local density decreased with the proportion of residential area, while it increased with the other factors (Table 5.2). The coefficients for area-specific factors indicated that local densities for Kushiro were overall larger than those for Boso, and local densities for Yamanashi were overall smaller than those for Boso (Table 5.2). The confidence intervals of the coefficients for all explanatory variables did not include zero, indicating that the effects were all statistically meaningful. The coefficient of determination (R^2) for the model was 0.43.

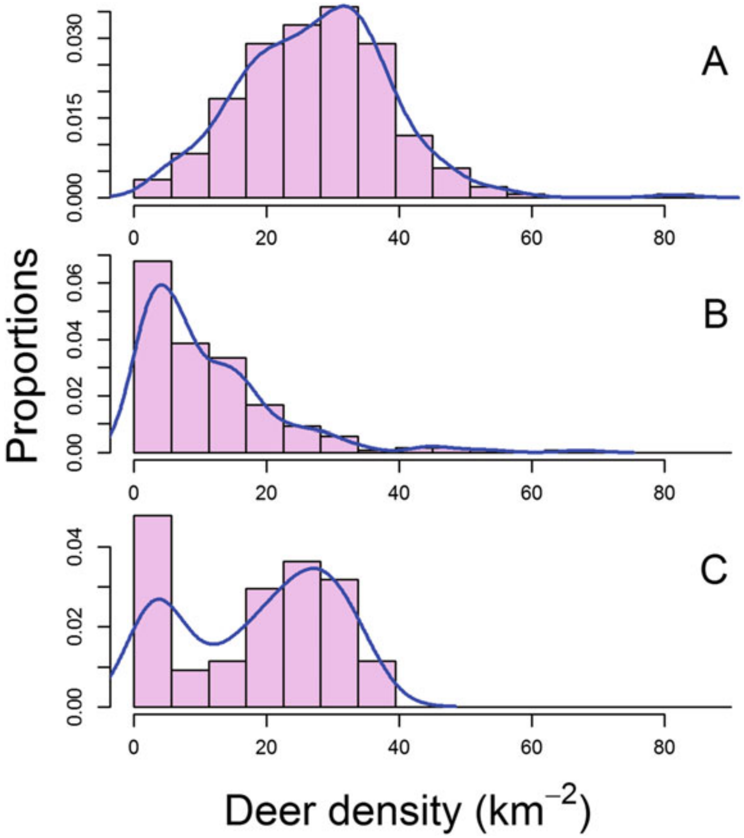

Fig. 5.3 Histogram of annual mean local density of sika deer during 2005–2012 in the three areas of Japan. A: Kushiro, B: Yamanashi, C: Boso

5.3.3 Effects of Environmental Conditions on Local Density

The mean values for the landscape variables selected in the model differed between Kushiro and Yamanashi and Boso (Fig. 5.5). The rate of DBL in Yamanashi and Boso was slightly higher than that in Kushiro, while the rate of mixed in Kushiro was higher than those in Yamanashi and Boso. Therefore, the proportions of forest-related components did not greatly differ. However, the rates of artificial meadows in Kushiro were significantly higher than those in Yamanashi and Boso. Additionally, the rate of residential area for Yamanashi and Boso was significantly higher than that in Kushiro. The annual mean temperature increased in the following order: Kushiro $<$ Yamanashi $<$ Boso.

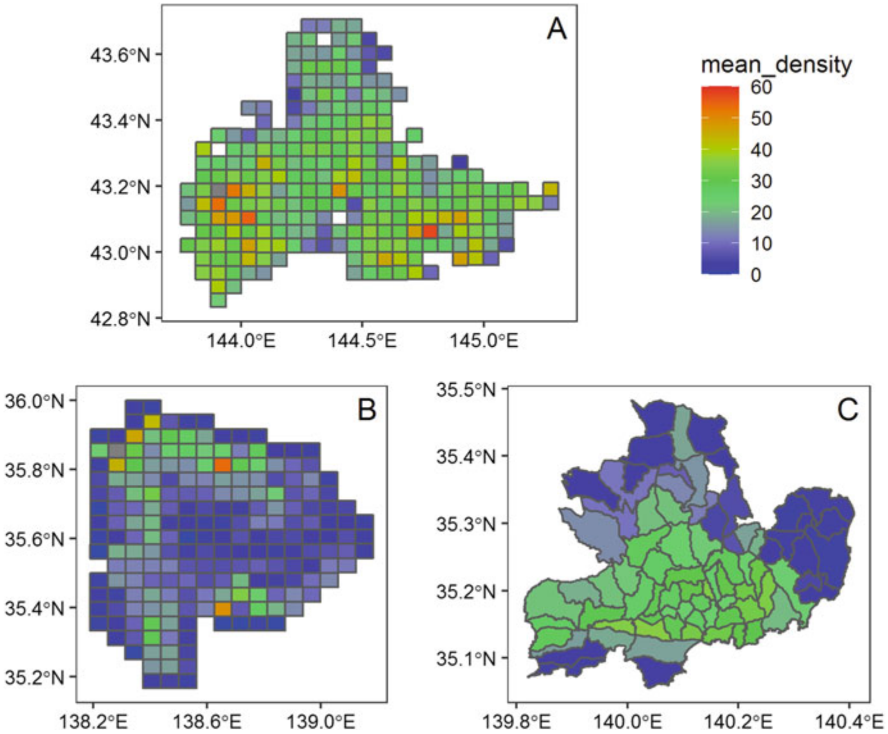

Fig. 5.4 Spatial map of the annual mean local sika deer densities during 2005–2012 in the three areas of Japan. A: Kushiro, B: Yamanashi, C: Boso

Table 5.2 Landscape and climate factors affecting the annual mean local density of sika deer during 2005–2012 in the three areas of Japan (Kushiro in Hokkaido, Yamanashi, and Boso in Chiba)

Exp. variables	Estimate	Std.Error	*t. value*	Pr(>|t|)	
Intercept (Boso)	3.80	3.63	1.05	0.294943	
DBL forest	11.32	2.25	5.04	6.41E–07	***
Mixed forest	20.96	3.51	5.97	4.25E–09	***
Artificial meadow	15.91	3.64	4.37	0.0000151	***
Residential area	−45.28	11.88	−3.81	0.000154	***
Mean temp	0.84	0.26	3.30	0.001042	**
Region (Kushiro)	11.33	2.61	4.34	0.0000174	***
Region (Yamanashi)	−4.06	1.82	−2.22	0.026535	*

"***" $Pr < 0.001$, "**" $Pr < 0.01$, "*" $Pr < 0.05$

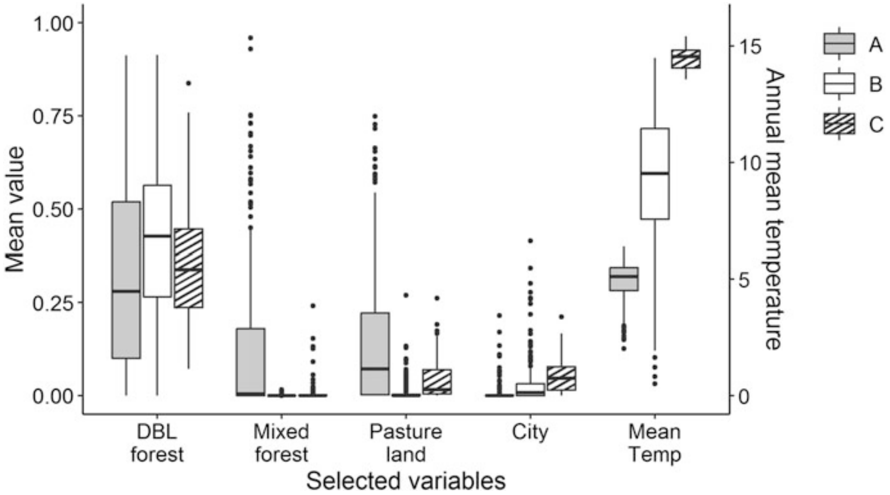

Fig. 5.5 Mean values of the variables selected for the best sika deer local density model for the three areas of Japan. A: Kushiro, B: Yamanashi, C: Boso

5.3.4 *Local Rate of Natural Increase in the Three Areas*

The distribution of the local finite rate of natural increase (λ) overlapped between the three areas (Fig. 5.6). The lowest value was 0.87, occurring in Yamanashi, while the highest rate was 1.67, occurring in Boso. The estimated rates for Kushiro were limited, with narrower ranges of 1.05–1.21. The estimates for several units exceeded potentially possible growth rate, that is, 1.36 or 1.46 possibly due to immigration in open populations, most of the estimates were within the potentially possible value in sika deer (1.36 for Matsuda et al. 1999, 1.46 for Hone et al. 2010, Iijima and Ueno 2016).

The model with the lowest AIC values included the following explanatory variables: (1) rate of evergreen forests, (2) annual mean temperature, (3) density dependence, and (4) area (Table 5.3). However, the confidence intervals of the coefficients for all explanatory variables included zero. Therefore, these effects are not discussed. The coefficient of determination (R^2) of the model was 0.14.

5.4 Discussion

5.4.1 *Landscape Factors Explaining Spatial Variation in Local Density*

Previous studies evaluated population densities at spatial scales ranging from 50 ha to thousands of square kilometers, although few have conducted inter-regional

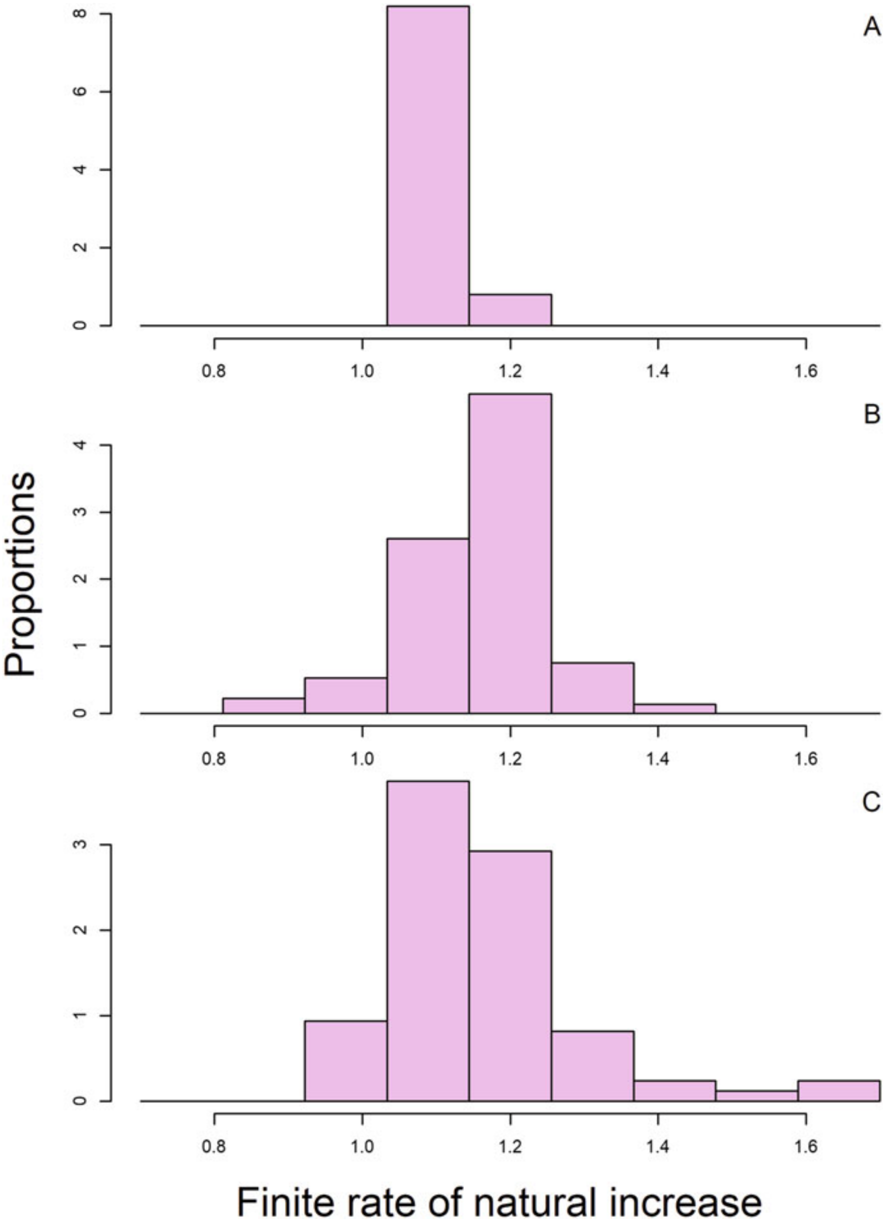

Fig. 5.6 Histogram of the unit-based finite rate of natural increase for the three areas of Japan. A: Kushiro, B: Yamanashi, C: Boso

comparisons for Japan. By comparing the estimated sika deer populations of the three areas, we revealed that the local density varied within areas, and the extent of variation overlapped between the areas, regardless of the different climatic

Table 5.3 Landscape and climatic factors, and population density affecting the spatial variations in the finite rate of natural increase in the three areas of Japan (Kushiro in Hokkaido, Yamanashi, and Boso in Chiba)

Exp. variables	Estimate	Std.Error	*t. value*	Pr(>|t|)	
Intercept (Boso)	1.08	0.03	34.62	< 2e–16	***
Evergreen forest	0.04	0.02	1.96	0.0501	.
Mean temp	0.00	0.00	1.56	0.1203	
Region (Kushiro)	−0.03	0.02	−1.48	0.1408	
Region (Yamanashi)	0.03	0.01	1.86	0.063	.
Density dependence	0.00	0.00	5.44	8.3E–08	***

"***" $Pr < 0.001$, "." $Pr < 0.1$

conditions. In consistent with our results, large spatial variations in local estimates at the scale of 3.3–82.6 km^2 have been reported in Kanagawa Prefecture, central Japan, where the deer density ranged from 1 to 54 deer/km^2 (Takeshita et al. 2017). Although many studies conducted in northern Japan reported high-density records exceeding 40 deer/km^2 in closed or semi-closed deer populations inhabiting islands or peninsulas (Takatsuki et al. 1991; Kaji et al. 2004), a recent estimate of the local density in an open deer population by distance sampling in Kushiro, Hokkaido, was 39.6 deer/km^2 (Uno et al. 2017). Therefore, our results suggest that a high density is locally possible, even in open populations. On Yakushima Island, southern Japan, the highest densities according to local estimates by distance sampling with a total length of 4 km or fecal pellet counting were 78 deer/km^2 (Agetsuma et al. 2003) and over 100 deer/km^2 (Koda et al. 2011), respectively. Therefore, a sika deer density of up to 40 deer/km^2 at the scale of dozens of square kilometers may be possible in any area of Japan, regardless of the different climate conditions.

The extent of local density was partly explained by the land uses within units. In this study, the proportions of DBLs, mixed forests, and meadows were selected as preferred habitats, while the proportion of residential area was negatively selected. Woodland is an important factor as it provides food and cover (Sakuragi et al. 2003; Morellet et al. 2011). Artificial meadows are also important landscapes as they provide food during non-snow seasons. Mysterud et al. (2002) reported that body mass is positively associated with the proportional area of meadows. Iijima et al. (2013) also demonstrated the importance of artificial meadows in the dynamics of a sika deer population using data from Yamanashi. Therefore, we reconfirmed the importance of forest and artificial meadows in explaining regional variation in deer density by incorporating data from other areas (Kushiro and Boso); Miyashita et al. (2008) reported that increases in forest edges in a landscape increased the probability of pregnancy in female sika deer. The length of the forest edge depends on a mosaic of artificial meadows and forests. As artificial meadows are replaced by flat areas of neighboring forests, the model selecting both forest and meadow factors may indicate the importance of forest edges.

As we could not consider season in our data analysis, the density estimate represents year-round values. However, the importance of woodland and meadow as food may vary seasonally, as meadows provide no food during the winter

(Morellet et al. 2011). By examining the seasonal estimates of density in future studies, we may separate the effects of forests and meadows on the regional variations in density.

A categorical factor, "Area," accounted for the spatial variations in deer density. A large–small relationship suggests a temporal difference occurring in the settling process. The population of sika deer has been increasing throughout Japan, with time lags. During the 1980s, harvest size in Hokkaido counted thousands compared to only dozens of deer harvested in Chiba and Yamanashi. During the late 1990s, harvest numbers have gone up a digit, though the relative difference was the same: Tens of thousands of deer in Hokkaido against hundreds of deer in Chiba and Yamanashi were shut for by hunting and nuisance control (https://www.env.go.jp/nature/choju/docs/docs2.html). Then, overabundance has become an issue in the 1990s for Hokkaido and 2000s for Honshu region (Asada and Ochiai 2009; Sakata et al. 2009; Uno et al. 2009). When harvest size represents abundance and distribution of sika deer, we can suggest that the settlement of deer distribution in Hokkaido is the oldest, which partly supports the order of the effect of area-specific factors.

5.4.2 Landscape Factors Contributing to the Differences in Global Density among the Three Areas

The global density for Kushiro was significantly larger than those of Yamanashi and Boso, although the extent of the local density overlapped between the three areas. This was attributed to the large number of units that consisted of favorable landscape elements for sika deer in Kushiro. The apparent difference in the total components of each unit among Kushiro, Yamanashi and Boso were attributed to the proportions of artificial meadows and residential area. Although the forest rate was an important factor affecting the local density, it was not a contributing factor to the difference among Kushiro, Yamanashi, and Boso. The mean temperature that exhibited a positive effect in the model increased in the following order: Kushiro < Yamanashi < Boso. However, it was not likely to affect the global density by area, as was the case for Yamanashi and Boso versus Kushiro. Additionally, the categorical factor of the area also likely increased the local density for Kushiro. Therefore, the global density in Kushiro was higher than that in Yamanashi and Boso because it contained a larger proportion of artificial meadows and smaller proportion of residential area, and the settlement period was longer.

5.4.3 Spatial Variations in Annual Population Growth

The intraspecific variation of ungulates in the northern hemisphere often exhibits a latitudinal trend (Herfindal et al. 2006). The wide range of latitudes covered by the

Japanese Archipelago, from 26°N to 45°N, has created a latitudinal tendency in food composition and a clear latitudinal cline in the body size of sika deer (Takatsuki 2009; Kubo and Takatsuki 2015). This may affect the spatial variation in the population growth of sika deer, as body size is related to important fitness components, such as the age at first reproduction, survival, and fecundity (Sæther et al. 1996), along with numerous morphological, physiological, and life-history traits (Fritz and Loison 2006). However, we did not identify statistically significant factors explaining the spatial variations in the estimates of population growth. The summary of the estimates was in the range of possible population growth rates for sika deer. Our pattern-oriented approach may not be appropriate for detecting latitudinal trends when compared to demography-oriented approaches (Bonenfant et al. 2009). A previous study suggested that the pregnancy rate of yearlings in a neighboring area of Kushiro recorded 90%, whereas 70% in a more Southern area such as Hyogo (Kaji et al. 2006; Yokoyama 2009). Such regional difference in reproduction may suggest the possibility of a latitudinal trend in population growth, which will be a future challenging topic that requires data from more regions.

5.4.4 Management Implications: Importance of Local Scale for Density Estimates

Hunting statistics of Japan are accessible via the internet, but are typically summarized by administrative units, i.e. a prefectural scale (http://www.env.go.jp/nature/choju/docs/docs2.html). The harvest size for Hokkaido prefecture which Kushiro belongs to was highest among all of the prefectures in Japan. However, an interregional comparison of hunting statistics without considering spatial scale is not appropriate. In this study, high-density units were clustered in all three areas, indicating that deer abundance is not spatially uniform, but structured. If we evaluated the population density at the prefecture scale, we might have concluded that the density for any area in Kushiro was much higher than those in Yamanashi and Boso. However, the deer density was locally diverse and partly explained by landscape elements. Therefore, the target density to effectively manage and predict sika deer populations should be determined at a local spatial scale (Chap. 34). Some sika deer in Hokkaido migrate seasonally, with the largest distance being approximately 100 km (Igota et al. 2004). However, their largest home ranges within seasons were approximately 6 km^2. Locality in activity has also been observed for moose in the USA, which exhibited an active boundary of 3 km^2 (Maier et al. 2005). Therefore, our spatial scale for estimating the local density (23–26 km^2 for Kushiro and Yamanashi, 1.2–35 km^2 for Boso) may have been reasonable in revealing spatial variations.

Although we stated that the local scale is appropriate for estimating abundance, management efforts for control measures, such as culling, should not be focused only on local areas. As deer can disperse and expand their distribution, inconsistent management operations between neighboring areas may not be effective in controlling open populations. Sika deer management in Japan is often based on management plans developed by prefectures and hunting and culling activities do not differ greatly between municipalities. Therefore, control measures should be implemented considering neighboring areas on a global scale.

In Japan, database for sport hunting is prepared at a scale of approximately 5 km square grid cell. However, the formats for database for nuisance control vary between prefectures. In some areas, the database lacks spatiotemporal data, while the spatial scales vary in others. As data for nuisance control are similar to the total harvest size, a consistent data format should be prepared for sika deer management.

In conclusion, we revealed that the sika deer density was spatially diverse within prefectures in Japan, and densities of up to 40 deer/km^2 at the scale of dozens of square kilometers may be possible in any area. Although variations in density within and between areas were partly explained by landscape elements, area-specific factors also explained the differences between areas, potentially due to the temporal difference in the settlement of distribution. Therefore, the targeted density for effectively managing and predicting sika deer populations should be selected based on a local scale. Data collection by 5 km square grid cells, as is already conducted for present hunting statistics in several areas of Japan, would be beneficial and should be expanded to other areas and cull data for nuisance control.

Further, new challenges to visualize population density and the number of harvests at a fine-scale such as settlement level have just begun in Hyogo Prefecture (Chap. 34).

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Chapter 6
Ecological and Evolutionary Response of Sika Deer Morphology to Varying Habitat Environments: From Body Size to Tooth Wear

Mugino O. Kubo

Abstract Sika deer in Japan are inhabiting various environments from northern subarctic coniferous forests to southern subtropical evergreen broad-leaved forests. This impacts sika deer morphology and contributes to their huge geographic variation. In this chapter, I review studies on geographical variation of sika deer morphology with reference to habitat environments. The Japanese sika deer showed significant variation among populations in body size, limb morphology, and craniodental morphology, which are partially associated with local adaptations to habitat environments. The body size of sika deer was strongly associated with climate condition, as hypothesized by Bergmann's rule, and additionally became larger in the areas with winter severity and high vegetation productivity as a consequence of phenotypic change in fat reserve. Significant morphological differentiation in mandibles and molars was found between northern and southern genetic lineages, tracing the evolutionary trends found in interspecific comparisons of grazing and browsing ruminants. This morphological change, especially inclement of molar height (hypsodonty), was related to consumption of graminoids (i.e., dwarf bamboo) by deer in the northern deciduous broad-leaved forests, which brought about accelerated tooth wear. Japanese sika deer is an ideal species for testing evolutionary hypotheses related to local adaptations.

6.1 Introduction

The sika deer (*Cervus nippon*) is widespread throughout eastern and northeastern Asia, from the Ussuri region of Siberia to northern Vietnam, Taiwan, and Japan (Ohtaishi 1986; Geist 1999). Because the distribution of the sika deer in the Japanese

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M. O. Kubo (✉)
Department of Natural Environmental Studies, Graduate School of Frontier Sciences,
The University of Tokyo, Kasiwa, Japan
e-mail: mugino@k.u-tokyo.ac.jp

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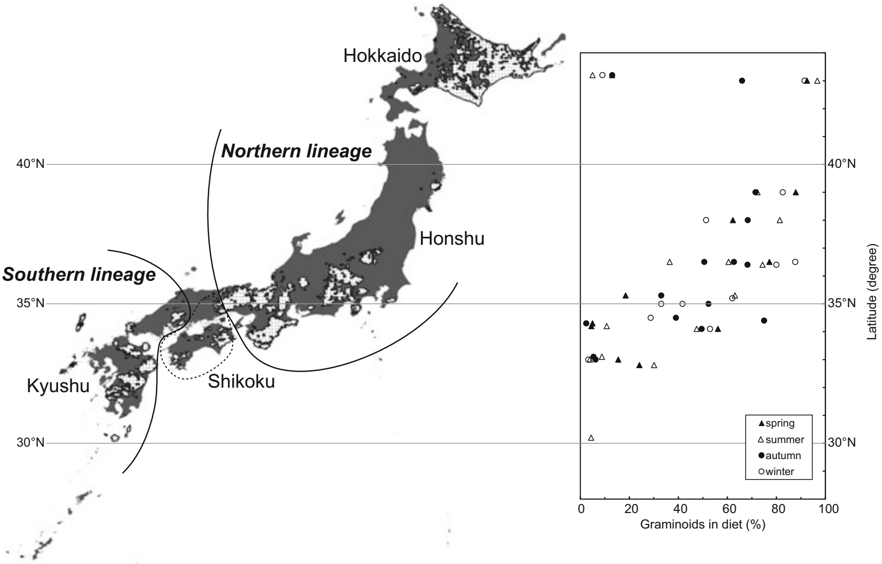

Fig. 6.1 Geographical distribution of the sika deer in Japan, along with its latitudinal variation in diet. The dotted areas of the left map are sika deer habitats. The solid lines represent the boundary between the two phylogenetic lineages: the northern lineage inhabits the area from Hokkaido to the central Honshu, whereas the southern lineage inhabits the southwestern part of Honshu, Kyushu, and the islets surrounding Kyushu. A possible hybridization area is located in central-western parts of Honshu and Shikoku. The scatter plot on the right shows latitudinal variation in the diet (modified from Takatsuki 2009). The x-axis represents the percentage of graminoids in the diet determined using quantitative dietary analyses of rumen contents or feces. This figure was originally published in Kubo (2014) and used under CC BY 4.0

archipelago extends from the northern to the southern islands (from 44°N to 26°N, Fig. 6.1), they inhabit a wide range of environments, from the northern, subarctic coniferous forests to the southern, temperate or even subtropical evergreen broad-leaved forests. Such variation in habitat has a strong influence on their ecology, involving feeding habits, seasonal migration, reproduction, and demography, which were summarized in detail in McCullough et al. (2009).

It is also widely acknowledged that Japanese sika deer show substantial variation in morphology (Ohtaishi 1986), which led to traditional classification into several subspecies of this species (Groves 2006; Ohtaishi 1986). However, this morphological variation was not fully described in McCullough et al. (2009) and shortly referred from the viewpoint of the subspecies classification in the chapters describing phylogenetic characteristics of sika deer (Nagata 2009; Tamate 2009). Through the contributions of phylogenetic studies from the mid-1990s to the early half of the 2000s, the researchers recognized the discrepancy between phylogeny and subspecies classification based on morphology. Japanese sika deer was divided into two genetic lineages, i.e., northern and southern lineages (Nagata 1999, 2009; Tamate et al. 1998; Goodman et al. 2001). The northern lineage includes populations in

Hokkaido and most of Honshu, except for the southwestern region (Fig. 6.1). The southern lineage includes populations in southwestern Honshu, Kyushu, and southwestern islands (e.g., Tsushima Island and Yakushima Island). The separation of the two lineages seemed to have occurred on the Asian continent ca. 0.3–0.5 mya, prior to their respective migration to the Japanese archipelago (Nagata 1999, 2009; Tamate et al. 1998). The subspecies classification based on morphology was not verified, and this discouraged further morphological investigation of local sika deer populations, unfortunately leaving behind several important evolutionary topics of local adaptations.

Since 2003, we have started comparative morphological studies of sika deer utilizing abundant culled individuals and specimens preserved in local natural history museums. We had two purposes at the beginning of this project: 1) to construct comparative osteological collection of sika deer covering most of local populations in Japan (Kubo et al. 2015) and 2) to investigate the relationship between ecology and morphology based on this collection. A review paper was issued previously covering the outcomes of the project (Kubo 2014). Together with related studies published after Kubo (2014), a synthetic review of morphological studies of sika deer is conducted in this chapter.

6.2 Latitudinal Variation in Body Size

One of the rationales to classify Japanese sika deer into several subspecies was their huge body size variation (Whitehead 1972; Ohtaishi 1986). Ohtaishi (1986) summarized body size variation in sika deer. Male deer in Hokkaido (previously mentioned as *C. nippon yesoensis*) weigh over 120 kg. Sika deer in Honshu (*C. nippon centralis*) showed a gradient from ca. 100 kg in northern area to ca. 60 kg in southwestern area. Sika deer in Shikoku and Kyushu (*C. nippon nippon*) are approximately 50 kg. Male deer in southern islands are much smaller than those in the northern part of Japan. For example, body weights for deer in Yakushima Island (*C. nippon yakushimae*) and deer in Kerama Islands (*C. nippon kerame*), which is an introduced population from Kyushu (Shiroma and Ohta 1996), are 35 kg and 30 kg, respectively. There seems to be a latitudinal cline in body size, which has been used as an example of Bergmann's rule. However, it has not been tested quantitatively. There have been several reports on geographic variation in the skull size among sika deer populations. Imaizumi (1970) described a latitudinal cline in skull size [condylobasal length (CBL)] for the purpose of species classification in what he termed the subgenus *Sika*. His taxonomic splitting of the sika deer into several species is not generally accepted (Ohtaishi 1986; Endo 1996). Imaizumi (1970) reported that *C. nippon* (most Japanese populations, except for Hokkaido, Yakushima Island, Kerama Islands, and Tsushima Islands) showed a cline in CBL that is larger in the north and smaller in the south. This regression slope was based on only seven individual males. Shiroma and Ohta (1996) compared skull morphology among eight populations (Hokkaido, Nikko, Kagoshima, Nozakijima Island, Tsushima Island, Mageshima Island, Yakushima Island, and Kerama Islands) and showed that the northernmost population (Hokkaido) had the largest skull size followed by Nikko, Kagoshima, and other island populations. Because the sampled populations were biased to island populations, it is still unclear whether the latitudinal cline followed Bergmann's rule. Together with the phylogenetic findings that the northern and southern lineages have independent evolutionary histories after divergence, the body size cline might merely reflect the fact that the northern lineage is currently occupying northern area in Japanese archipelago and the southern lineage is in southwestern area. Therefore, it should be taken into account the phylogenetic lineages.

Kubo and Takatsuki (2015) tested whether Bergmann's rule can be applied even when the correspondence between the phylogenetic lineages and their current habitat regions was considered. In total, 31 populations covering most of the sika deer population in Japan were analyzed, and their body mass and skull size [cranial greatest length (CGL)] were collected from published literature and direct measurements of the skulls, respectively, for males and females. Consistent with Bergmann's rule, a clear latitudinal cline of body size was found for sika deer. It was clarified that linear regression lines of body size measurement (body mass or CGL) against latitude were not significantly different between two phylogenetic lineages for both sexes. Therefore, the intraspecific phylogeny did not significantly affect body size (but this was not the case for mandibular morphology, which will be explained in the following section of this chapter), and the latitudinal cline in body size seemed to associate with the current latitudinal variation of habitat environments.

Kubo and Takatsuki (2015) further investigated the effects of environmental variables on body mass variation using path analysis, the statistical analysis which could clarify inter-variable relationships and estimate direct and indirect effects of environmental variables on body size. To construct path models, they focused on the following ecological hypotheses pertaining to Bergmann's rule in mammals: (1) heat conservation, (2) heat dissipation, (3) starvation resistance, (4) food availability, and (5) insularity. According to these hypotheses, relevant environmental variables were collected for each of the 31 populations, i.e., mean annual temperature, annual precipitation, the normalized difference vegetation index (NDVI), and Kira's coldness index (CI). Path analyses showed that mean annual temperature and annual precipitation had significant negative effects on body size, and the annual temperature had the greatest effect among tested environmental variables (Fig. 6.2). Winter severity (CI) and food availability (NDVI) during spring were significantly associated with body mass in a positive direction but not with CGL. Both heat conservation and dissipation hypotheses were accepted, and food availability and starvation resistance hypotheses were applicable to variation of body mass but not to CGL, indicating that phenotypic changes in fat reserves strongly influence variation in body mass. Path diagram modeling of inter-variable relationships fit well for females but not for males, and unexplained variation of male body size suggested the presence of unidentified factors. In other words, un-hypothesized ecological factors varying with latitude affect male body size variation. It is plausible that variation in mating systems among populations may play a role (Miura 1984). It is possible that

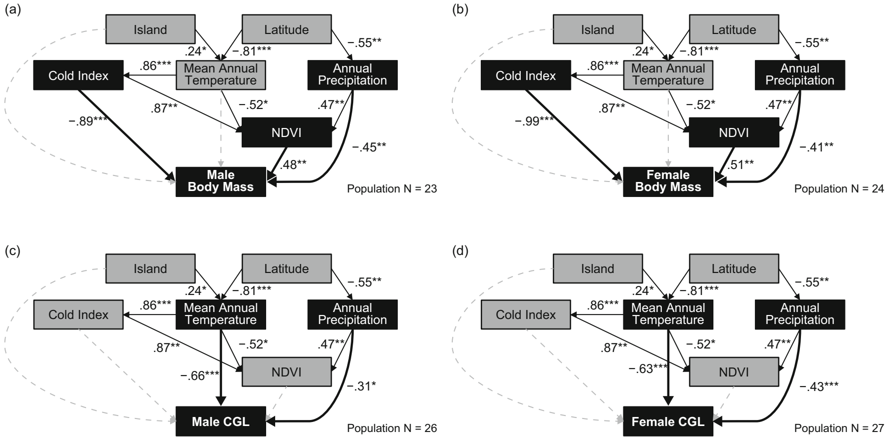

Fig. 6.2 Path diagrams explaining causal relationships between environmental factors and body size (a, male body mass; b, female body mass; c, male CGL; d, female CGL) in the sika deer. The figures next to the arrows are the standardized partial regression coefficients. Significance of relationships is indicated by asterisks as follows: $^{*}P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$. Modified from Kubo and Takatsuki (2015)

male deer from the dense evergreen forests that dominate southern Japan may not have large reproductive territories or harems, and intermale competition during rutting may be moderated. Such conditions may not favor larger body sizes of males.

6.3 Variation in Limb Morphology

In the sika deer, postcranial morphological traits have been less investigated because most specimens of the sika deer preserved in museums are limited to skulls and mandibles. Based on measurements of the culled sika deer of a northern population, Takatsuki (1992) showed that the sika deer cannot live in areas with heavy snowfall, where snow accumulates at a level higher than the limb length of the sika deer. Ochiai and Asada (1995) reported a growth pattern of the body size of the sika deer from a population in a temperate region (Boso Peninsula, 35°N 140°E) and found that the hind limb length was relatively (compared with shoulder height) shorter than that of other northern populations. This finding implies that the amount of snowfall or habitat closedness may influence variation in the hind limb length. In the subsequent paper, Ochiai and Asada (1997) compared the size of the skull and limb bones of the Boso population with those of a northern population (Nikko, 36°N 139°E). It was shown that the limb length was proportional to $(\text{body mass})^{0.24}$, thus confirming the biomechanical prediction of McMahon (1973), which predicts an allometric relationship; the limb length is proportional to $(\text{body mass})^{0.25}$. These data also implied that the positive deviation of the Nikko deer from the allometric prediction line can be explained by snow depth of the habitat.

Lately, Terada et al. (2012) showed morphological differentiation in limbs among southern island populations of the sika deer. They used eight populations belonging to the southern lineage and measured both the skull size (CBL) and the length of limb bones (scapula, humerus, radius, metacarpus, femur, tibia, and metatarsus). They showed that there was significant variation in the measurements among the populations, particularly in CBL and the metacarpal length. In analyses, they regressed the log-transformed metacarpal length against log-transformed CBL (a proxy of the body size) and obtained the regression slope and intercept for each population. The slope did not differ significantly among the populations and had a value of 0.74, which was significantly smaller than 1 (i.e., negative allometry). This value is close to the biomechanical prediction as well as to the empirical regression slope obtained for other sika deer populations (Ochiai and Asada 1997), provided that CBL is isometric to body mass ($CBL^3 = $ body mass).

On the other hand, the regression intercept (relative carpal length adjusted for the body size) negatively correlated with habitat topology. This was quantitatively evaluated using a geographical information system (GIS), the steeper the habitat area, the shorter the metacarpal length. As Terada et al. (2012) discussed in their paper, this result is in agreement with the interspecific pattern of bovid species; species in mountainous habitats have shorter limbs than those in open habitats (Scott 1985, 1987). Since annual snowfall is less than 5 cm for the studied habitats of sika deer, Terada et al. (2012) discussed that shorter metacarpal might be favored because it can increase stability in rugged terrain. The relationship between habitat topology and limb morphology has not been studied in other populations, particularly in those of the northern lineage. Together with the observations of Takatsuki (1992) and Ochiai and Asada (1997), it is expected that limb morphology of the northern sika deer is affected by both habitat topology and the amount of snowfall. This topic is to be investigated in the future.

6.4 Variation in Craniodental Morphology

Based on prior interspecific comparative studies in ruminants, a number of morphological characteristics have been shown to correlate with grazing: e.g., broader snouts, larger areas for the insertion of the masseter muscle, longer diastemas, shorter premolar rows, and higher mandibular corpora (reviewed in Janis 1995). Some of these morphological characteristics were not statistically different after adjusting for phylogeny; however, molar row volume, molar hypsodonty (relative height of unworn molar against its buccolingual width), and masseter muscle mass were still significantly larger in the grazing species after adjustment (Pérez-Barberea and Gordon 1999; Williams and Kay 2001; Clauss et al. 2008). These morphological characteristics have been interpreted as adaptations to ingesting and masticating a relatively larger amount of less nutritious, more fibrous, and abrasive graminoids compared with browsers or intermediate feeders.

Japanese sika deer shows considerable variation in food habits according to their local habitat environments (reviewed in Takatsuki 2009). Previous studies of the food habits of the sika deer have provided quantitative and comparative data through analyses of rumen contents or feces (Fig. 6.1). Sika deer populations inhabiting the subarctic coniferous forests or the cool-temperate deciduous broad-leaved forests subsist mostly on graminoids, particularly dwarf bamboo (e.g., *Sasa nipponica*), which is dominant within the understories of these forests. Thus, these northern populations can be categorized as "grazers" inhabiting closed habitats (Hofmann 1985). On the other hand, the sika deer that inhabit the temperate evergreen broad-leaved forests feed mainly on the leaves of woody plants, and they are classified as either "intermediate feeders" or "browsers." Most populations in the southern lineage are browsers or intermediate feeders, whereas those of the northern lineage show a larger variation from grazers to intermediate feeders. Based on this information, there are two different levels at which microevolutionary hypotheses can be tested in Japanese sika deer: between the two phylogenetic lineages and among populations within each lineage. The latter reflects a more recent divergence than the former and, specifically here, the eco-morphological differentiation between grazer and intermediate feeder in the northern lineage. In this point, Japanese sika deer was ideal for testing the relationship between craniodental morphology and feeding habits, as proposed in the interspecific comparisons.

Ozaki et al. (2007) and Kubo (2014) examined the morphology of sika deer mandibles and teeth collected from all over the Japanese archipelago. Mandibles of more than 600 female sika deer from 11 populations of the northern lineage and 6 populations from the southern lineage were used (Table 6.1). Among 15 measurements related to masticatory function (Fig. 6.3), the measurements related to the cheek tooth size [lengths of the cheek tooth row, molar row, and premolar row; breadths of lower first molar (M_1) and second molar (M_2); length of lower third molar (M_3) and M_3 hypsodonty], mandibular height, and diastema length were significantly different between the two lineages after adjusting for mandibular size ($P < 0.05$). The northern lineage had larger and more hypsodont (high-crowned) cheek teeth, higher mandibular corpus, and shorter diastema than those of the southern lineage. On the other hand, these measurements were not significantly different between grazer and intermediate feeder populations of the same lineage, except for the mandibular corpus height, which was larger in the grazers. In addition, a significant difference between grazer and intermediate feeder populations was observed in the ascending ramus height.

Significant differences between the two lineages were observed in the cheek tooth size. The northern lineage had a buccolingually wider and mesiodistally more elongated cheek tooth row than those of the southern lineage. This result implies that the ancestral population of the northern lineage may have acquired a larger occlusal surface area of cheek teeth, which was adaptive for grazing. The shorter diastema of the northern lineage seems to be associated with the elongation of the cheek tooth row. The occlusal area of the cheek tooth row and M_3 hypsodonty were significantly increased in the northern linage. This result implies that the ancestral population of the northern lineage may have adapted to abrasive diets, possibly in a

Table 6.1 Sika deer populations used in the analyses of mandibles and molar wear rate

Genetic lineage	Population	Proportion of grass in diet (%)	Feeding type	No. of adult specimens (mandibles)	No. of specimens (molar wear rate)
Northern	1. Eastern Hokkaido	46.3	Grazer	65	98
	2. Mt. Goyo	52.5	Grazer	53	67
	3. Kinkazan Island	65.8	Grazer	48	48
	4. Ashio	90.0	Grazer	35	24
	5. Nikko	73.9	Grazer	34	36
	6. Boso Peninsula	45.2	Intermediate feeder	59	66
	7. Okutama	32.1	Intermediate feeder	21	32
	8. Tanzawa	–	Intermediate feeder	47	–
	9. Yamanashi	42.2	Intermediate feeder	13	20
	10. Izu Peninsula	30.5	Intermediate feeder	39	59
	11. Nara Park	81.4	Grazer	36	38
Southern	12. Shimane	38.1	Intermediate feeder	17	18
	13. Yamaguchi	6.5	Browser	24	28
	14. Tsushima Island	3.4	Browser	28	35
	15. Fukuoka	7.2	Browser	21	28
	16. Mt. Shiraga	25.6	Intermediate feeder	53	82
	17. Yakushima Island	4.4	Browser	8	23

continuous or a recurrent harsh environment during the last glacial period, when possible colonization into Japan considered to have taken place (Ozaki et al. 2007).

On the other hand, the cheek tooth size (length, breadth, and height) was not significantly different between grazer and intermediate feeder populations of the northern lineage. This finding indicates that a further increment of the cheek tooth size may not have occurred in grazer populations. The ascending ramus height was significantly greater in grazer populations. The higher ascending ramus may be

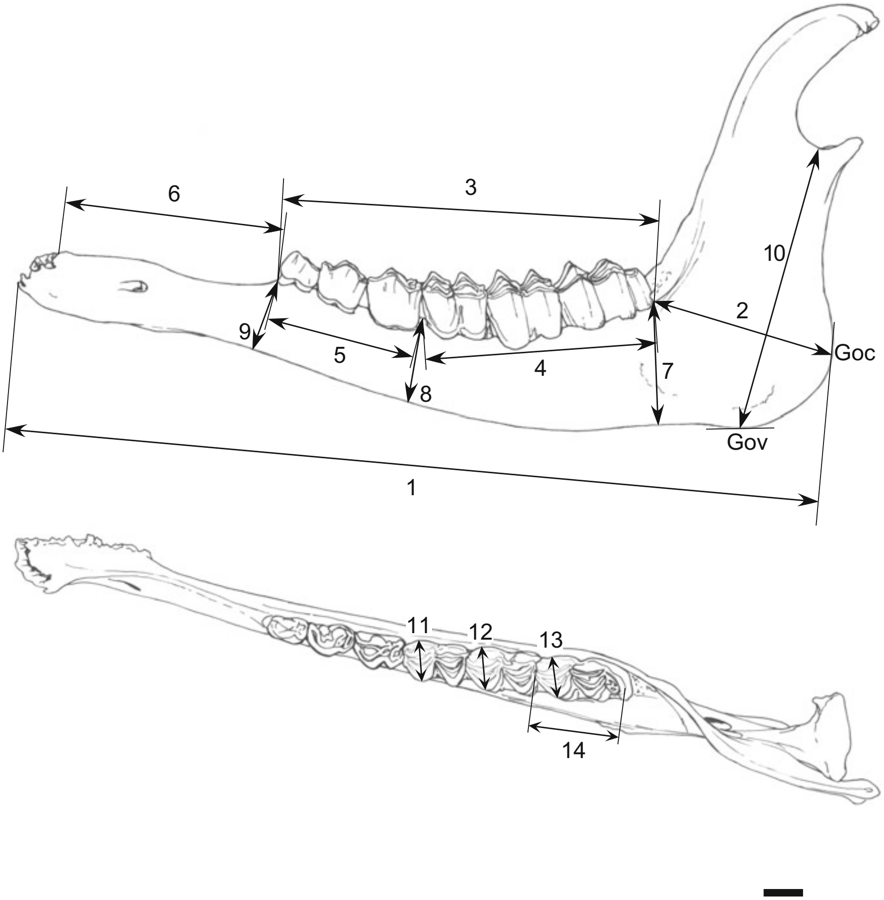

Fig. 6.3 The 15 measurements of mandibles of the sika deer: (1) greatest length of the mandible; (2) mandibular angle length; (3) cheek tooth row length; (4) molar row length; (5) premolar row length; (6) diastema length; (7) height of the mandible behind M_3; (8) height of the mandible in front of M_1; (9) height of the mandible in front of P_2; (10) GOV_NO, gonion ventrale to the deepest point of the mandibular notch; (11) breadth of M_1; (12) breadth of M_2; (13) breadth of M_3; (14) length of M_3; (15) height of unworn M_3 (not shown); and GOC, gonion caudale. Scale bars are 1 cm. This figure was originally published in Kubo (2014) and used under CC BY 4.0

associated with a larger area for the insertion of the masseter muscle, which was adaptive for masticating fibrous graminoids.

Two hypotheses may explain the difference between the results of between-lineage comparison and between-feeding-type comparison. One is that the ancestral population of the northern lineage may have acquired both larger cheek teeth and a higher ascending ramus, but under the current condition of relaxed selective pressure, the ascending ramus of intermediate feeder populations has shrunk, whereas the cheek tooth size has not changed yet (i.e., a slower evolutionary response of cheek teeth). Another is that the ancestral population of the northern lineage may have acquired a larger cheek tooth size but not a higher ascending ramus. In populations of the northern lineage, the significant difference in the ascending ramus between grazer and intermediate feeder populations merely reflects a phenotypic (i.e., not evolutionary) response to a diet comprised of a larger amount of fibrous graminoids, which is known based on developmental experiments on laboratory animals reared on hard diets (Ito et al. 1988).

6.5 Variation in Tooth Wear

As reviewed in the above section, sika deer showed significant variation in diets among local populations. Variation in consumption of silica-rich graminoids had strong influence on tooth wear. Grazing populations of sika deer should show faster tooth wear rate than browsing or intermediate-feeding populations. We have investigated the relationship between graminoid consumption and tooth wear rate using 16 sika deer population (Ozaki et al. 2010; Kubo 2014; Kubo and Yamada 2014). For all of the investigated deer, age at death were assessed by tooth eruption condition for infants and yearlings and histological analysis of cementum annuli in incisor roots for adults. Linear regression of log-transformed M_1 against age at death was conducted for each deer population (Fig. 6.4).

Significant variation of M_1 wear rate was found among the populations. The northern lineage populations in general showed faster wear rate than the southern lineage populations, but both showed intra-lineage variation. Specifically, grazing sika deer showed faster molar wear than browsing and intermediate-feeding

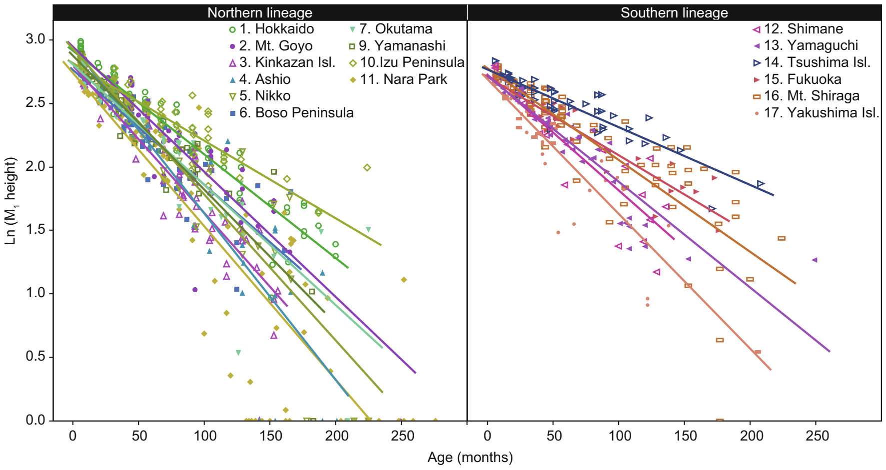

Fig. 6.4 Comparisons of molar wear rates in the female sika deer among 16 populations with different food habits. Two phylogenetic lineages are presented separately. Key as in the plots

populations. This was further proven by correlation analysis between the regression slope (M_1 wear rate) and proportion of graminoids in diet, indicating that a larger amount of graminoid consumption is positively associated with a faster wear rate. On the other hand, it was also shown that the molar wear rate and the M_3 hypsodonty were positively correlated (Kubo and Yamada 2014). This implied an evolutionary increment in the molar height corresponding to the molar wear rate. However, this conclusion should be reserved because the degree of hypsodonty differed significantly between the northern and southern lineages, as we saw in the preceding section. If we considered the relationship, respectively, in each lineage, the hypsodonty increased with the accelerating molar wear rate in the southern lineage but not in the northern lineage. Genetic evidence indicated that the greatest genetic differentiation was found among populations of the southern lineage, implying local adaptation of increasing hypsodonty may have occurred in the southern lineage. On the other hand, among populations of the northern lineage, the genetic differentiation occurred more recently because of habitat fragmentation. Therefore, according to the findings of comparative analyses of mandibles, we hypothesize that the ancestral population of the northern lineage acquired more hypsodont molars in the past, possibly under strong environmental pressure that promoted molar wear. We also hypothesize that after subdivision into local populations, molar height did not change measurably because of relaxed selection and/or insufficient duration of selection, particularly in populations of the northern lineage.

Phytoliths (silica body) in graminoids have been considered as one of the causal factors of tooth wear in herbivorous mammals (Janis and Fortelius 1988). If so, we expect traces of abrasion by phytoliths on the tooth surface at a microscopic level. Microscopic wear on animal teeth is called as microwear and used widely in palaeontology and palaeoanthropology to estimate diets of extinct species (Walker et al. 1978; Teaford 1988; Scott et al. 2005). Interspecific comparisons of dental microwear among herbivorous ungulates (artiodactyls and perrisodactyls) revealed that diets with different physical properties left different microwear (Solounias and Semprebon 2002; Solounias et al. 1988; Schulz et al. 2010; Schulz et al. 2013). Grazers had tooth surfaces with abundant aligned scratches, whereas browsers had fewer scratches but many pits. This relationship can be qualified explicitly by intraspecific comparisons, as less confounding factors (i.e., differences in mastication mechanism, chewing behavior, body and tooth size) are involved in the comparisons among populations of a single species. Kubo et al. (2017) investigated dental microwear differences among sika deer populations, and lately Kubo and Fujita (2021) corroborated Kubo et al. (2017) findings and showed correlation between diets and dental microwear, aiming to apply the relationship to estimate the diet of extinct insular deer in Okinawa Island. According to their analyses, the grazing deer had more undulated tooth surface with abundant scratches, whereas the browsing deer had flatter surface with less scratches (Fig. 6.5). The variables quantifying surface roughness (e.g., International Standard ISO 25178-2) were higher in the grazing sika deer.

From the above findings, we can realize how the microscopic tooth wear can be accumulated to bring about differential tooth wear rate, which further might have

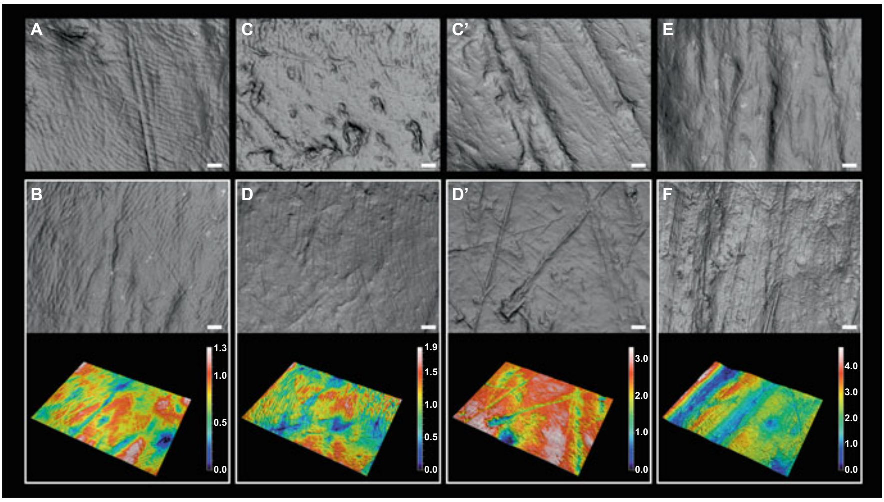

Fig. 6.5 Dental microwear images of extant sika deer in different localities. Upper row shows 2D micrographs of tooth surfaces and lower row shows both 2D micrographs and 3D surface models. Browsing sika deer [A: TS-5878 (Locality No. 14); B: TPM-M316 (Loc. No. 17)]. Mixed feeding sika deer [C: YN-0505; C′: YN-0512 (Loc. No. 9); D: SO-0422; D′: SO-04100 (Loc. No. 10)]. Grazing sika deer [E: TG-0517 (Loc. No. 5); F: MGK-9435 (Loc. No. 3)]. Note that more undulated tooth surface with abundant scratches is characteristic for grazing sika deer. Locality no. of each specimen is corresponding to that appeared in Table 6.1. The white bar in the 2D micrographs indicates 10 μm. For B, D, D′, and F, 3D surface models are shown with the vertical scales (the unit of the scale is μm)

cause evolutionary increase of tooth height. Comprehensive investigation of ecology and tooth wear relation in sika deer can contribute to evolutionary ecology and morphology of mammals.

6.6 Future Perspectives

Studies of morphological comparisons using the Japanese sika deer were reviewed in this chapter. Several conclusions can be drawn: 1) selective pressures—climatic conditions, topographical features of a habitat that require climbing ability, or accelerated tooth wear associated with grass consumption—promote the local adaptation of populations; 2) in some cases, genetic divergence among local populations is insufficient in duration, resulting in a smaller extent of morphological change compared with that in subspecific lineages or closely related species; and 3) a phenotypic change resulting from nutritional conditions affects to some extent, depending on traits (as we have seen in association between body mass and habitat environments).

There are still several traits to be investigated for intraspecific variations or trends in the sika deer. For example, geographical variation in the size and morphology of antlers is an attractive topic with reference to the evolution of antlers in Cervidae (Gould 1974; Geist 1999). Miura (1984) reported geographical variation in mating behavior among local populations. This implies that habitat closedness may have a strong impact on the degree of aggregation and thus the mating system of the sika deer. This is in agreement with the evolutionary trend observed across ruminant species (Jarman 1974; Pérez-Barberea et al. 2002). Whether this variation in the mating system is related to antler variation among local deer populations is another intriguing question.

As the craniodental studies reviewed in this chapter were focused on feeding habits, other morphological aspects of cranial morphology are to be investigated. For example, variation in endocranial (brain) size and morphology is an attractive theme concerning sensory functions. This should be a rewarding topic, though it requires intensive laboratory work of CT scanning of the sika deer collections housed in museums. Also, postcranial skeletons are to be further studied, as mentioned in this chapter, from the perspective that they also exhibit an evolutionary and ecological response to various habitat environments.

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Chapter 7
Reproductive Variation of Sika Deer

Yukiko Matsuura

Abstract Sika deer have wide variations in pregnancy rates, gestation periods, and birth/conception periods according to nutritional condition relating to deer density. In this chapter, I review the variation in these reproductive characteristics of sika deer. Pregnancy rates of young females tend to vary with nutritional stress. In Hyogo Prefecture, the pregnancy rate of yearling decreased from 76.6% to 15.6% due to limited food resources. There is not enough data to assess variation of birth weight within populations; birth weight varies from 3 kg to 7 kg in Japan as a whole, with large regional variation. Birth/conception periods estimated by fetal growth vary with a range of 100 days in Hokkaido and 150 days in Hyogo Prefecture. Late births seem disadvantageous for fawns and mothers, but they sometimes occur. Late births result from late conception and prolonged gestation. This is remarkable in young or nutrition-poor females in harsh winters because they are more susceptible to environmental stress. Eighty percent of pregnant females have plural corpora lutea in the ovaries, which is formed at ovulation after conception. The plural corpora lutea are part of a physiological mechanism that allows sika deer to maintain high fertility.

7.1 Introduction

Pregnancy, birth, and lactation require more energy than is required to maintain normal body functions. Therefore, it is advantageous for deer to give birth when food resources are abundant and high in quality (Bronson 1989). The habitats in higher latitudes are characterized by more significant changes in plant phenology, limiting the suitable time for fawning. However, variation in conception and birth periods of approximately 50–100 days has been reported in northern deer species including white-tailed deer (*Odocoileus verginianus*, Verme 1965) and red deer (*Cervus elaphus*, Mitchell and Cubby 1981). Sika deer (*Cervus nippon*) in Japan also exhibit a wide range of conception/birth periods, over 100 days (Suzuki et al.

Y. Matsuura (✉)
Hokkaido Research Center, Forestry and Forest Products Research Institute, Sapporo, Japan
e-mail: ymtur@affrc.go.jp

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1996; Koizumi et al. 2009; Matsukane and Yokoyama 2018). Births outside of the optimal period can increase offspring mortality and decrease female reproductive success. Therefore, selection should function to eliminate births outside of the optimal period, in contrast to the wide variation observed in nature. In addition to birth timing, variation in birth weight and pregnancy rate, which are directly related to population changes, has also been observed, indicating that optimal traits are not always conserved in nature.

In this chapter, I review the variation observed in the reproductive traits of sika deer and contributing factors to these variations. I also discuss the reproductive physiology of sika deer, focusing on the corpus luteum, which forms in the ovary as a factor contributing to high pregnancy rates in this species.

7.2 Pregnancy Rate

In sika deer, pregnancy rates are basically determined by the presence of a fetus or fetal sac in the uterus of killed females but may also be confirmed by signs of lactation or regression of the corpus luteum (Matsukane and Yokoyama 2018). Pregnancy rates remain high in middle-aged and older females, whereas those of young females tend to vary with nutritional stress. In Hyogo Prefecture, the pregnancy rates of yearling females decreased from 76.6% in 1988–1992 (Koizumi et al. 2009) to 15.6% in 2003–2016 (Matsukane and Yokoyama 2018). By contrast, the pregnancy rates of deer aged ≥ 2 years were relatively constant, with approximately 89.4% in 1988–1992 (Koizumi et al. 2009) and 80% in 2003–2016 (Matsukane and Yokoyama 2018). Matsukane and Yokoyama (2018) suggested that deer density has increased since 2003 and that the severe decline in understory vegetation was reflected in a decline in yearling pregnancy rate. Because yearlings are in the growth stage, they are more susceptible to environmental influences; thus, limited food resources can prevent yearlings from reaching the physiological level necessary to attaining estrus and become pregnant. As the deer density increases, the proportion of such individuals also increases, resulting in a lower pregnancy rate among yearlings and extending the primiparous age of the population.

The adult pregnancy rate is additionally affected by deer density, but to a smaller extent than that observed in yearlings. On Nakanoshima Island, Hokkaido, sika deer have experienced repeated population irruptions since the introduction of three deer in the 1950s. During the first irruption from 1982 to 1984, none of the 11 marked deer with the age of 2 years old had fawns suggesting delayed age at maturity (Kaji et al. 1988, Chap. 17). Due to chronic high density, these deer have experienced a long-term shortage of food resources. As a result, 1- and 2-year-old females stopped conceiving, such that the age of sexual maturity is approaching 3 years in this population. By contrast, the pregnancy rate of deer aged >3 years has remained high, reaching 70% around 2001, at a deer density of >80 animals/km^2 (Kaji and Takahashi, unpublished data). Thus, density-dependent changes in the pregnancy rate were more pronounced among young animals in this population. Sika deer pregnancy rates may also be affected by decreases in deer density. On Nakanoshima Island, the pregnancy rate recovered quickly when the deer density was reduced. From 2012 to 2014, a large-scale population culling program was conducted, reducing the deer density from an estimated 55/km^2 in 2012 to 11/km^2 by the end of 2014. As a result, a pregnant 2-year-old female was found in the winter of 2012, and the pregnancy rate of deer aged $\geq$3 years reached 100% by 2014 (Y Matsuura et al. unpublished data). In this case, the pregnancy rate changed first in 2-year-old females. In large herbivores, density effects first affect early survival, followed by age at sexual maturity (Eberhardt 2002; Bonenfant et al. 2009). Thus, the reproductive status of young females may be an indicator of qualitative population changes. If the nutritional status is good, then the yearling pregnancy rate will also be high. In eastern Hokkaido, the yearling pregnancy rate was reported to be 83.3% (Suzuki and Ohtaishi 1993). In such areas, the deer population will increase in the following year by the number of females aged $>$1 year, resulting in a significant population increase.

In Japan, there have been no reports of pregnancy among fawns, although one case was suspected following histochemical observation of a regressed corpus luteum in the ovary of a yearling killed in January in northern Hokkaido (Y Matsuura, unpublished data). The corpus luteum forms during estrus and is maintained throughout gestation. In this case, the regressed corpus luteum was assumed to have been caused by pregnancy during the mating season when the deer was a fawn, presumably followed by birth in the early summer of her first year. Because fawn pregnancies have been reported in sika deer introduced to the USA (Feldhamer and Marcus 1994), it is clear that fawns can become pregnant if their nutritional status is good. However, we observed $>$1400 uteri/ovaries within the same region but only one suspected case of fawn pregnancy, indicating that this is a rare phenomenon if it occurs.

The impact of aging on pregnancy rates is difficult to assess because there are few old deer within the population. In Hyogo and Kumamoto prefectures, the pregnancy rates of deer aged $\geq$10 years have been reported to be high, 86.6% and 92%, respectively (Koizumi et al. 2009). In Iwate Prefecture, the pregnancy rate of deer aged $\geq$11 years ($<$ 20%) was lower than that for aged 2–10 years ($>$ 80%) according to a figure in Takatsuki (2006). The highest ages at which pregnancy has been observed in sika deer were 16 years in eastern Hokkaido (Kaji 2001), 17 years in Hyogo (Koizumi et al. 2009), and 16 years in Kumamoto (Koizumi et al. 2009).

7.3 Gestation Period

The gestation period of sika deer has been reported to range from 224 days, based on hormonal changes (Matsuura et al. 2004a), to 231 days, based on behavioral observations (Ohnishi et al. 2009). The gestation period also varies according to environmental conditions, with younger, lower-weight females having a longer gestation period in years with severe winter conditions (Matsuura et al. 2004b). In white-tailed deer (*Odocoileus virginianus*, Verme 1965) and caribou (*Rangifer tarandus*, McEwan and Whitehead 1972), the gestation period of individuals with poor nutritional status is also prolonged. Lighter-weight females and those with poor nutrition are more susceptible to harsh environmental conditions and have lower fetal growth rates (Kobayashi et al. 2004). Therefore, I speculate that prolongation of the gestation period allows fetuses to grow to larger sizes.

7.4 Birth Weight

Birth weight varies according to region and nutritional status; however, these data are scarce due to the difficulty of capturing newborns immediately after birth. Estimates are based on the measurements of fetuses captured during the birth season indicating that sika deer birth weights are typically about 6000 g in eastern Hokkaido (Suzuki and Ohtaishi 1993) and 4000 g in Hyogo Prefecture (Koizumi et al. 2009). In northern Hokkaido, a fetus was found to weigh 6850 g, whereas a fawn captured immediately after birth weighed 6400 g (Y Matsuura, unpublished data). These findings imply variation in birth weight among Hokkaido sika deer. On Kinkazan Island, Miyagi Prefecture, where many newborn fawns have been captured and measured, the average birth weight was estimated to be 3380 g for males and 3070 g for females, suggesting lower birth weights than in other areas due to high deer density (Ohnishi et al. 2009).

Cases of dystocia caused by fetomaternal disproportion were observed on Nakanoshima Island from 1993 to 2002, when the deer population was at high density (Takahashi et al. 2005). In these cases, the proportion of the fetal skeleton to the maternal skeleton was large; long-term restriction of food resources is thought to limit maternal growth, whereas its effects on fetal growth appear later. Notably, most of these cases occurred in primiparous females, suggesting that the depletion of food resources due to high deer density delayed pelvic growth.

7.5 Birth and Conception Periods

Birth and conception periods have been estimated using a fetal growth model based on fetal measurements (Suzuki et al. 1996; Yanagawa et al. 2015). In eastern Hokkaido, the conception period was estimated to be from October 7 to January 17, varying over a range of about 100 days, with a peak from mid-October to early November (Suzuki et al. 1996). The conception period in Hyogo Prefecture was estimated to be from late August to early January, varying over a range of 150 days, with a peak in mid-September (Matsukane and Yokoyama 2018). Thus, the conception period started about 1 month earlier in Honshu than in Hokkaido. In both areas, late conception was estimated to occur in January, producing much later births than normal. In Hokkaido, the peak birth season is in June. Figure 7.1 shows the

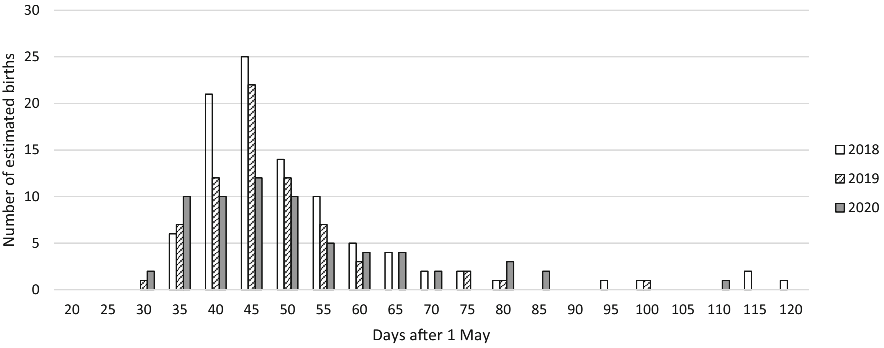

Fig. 7.1 Distribution of birth periods of sika deer in Nishiokoppe region over 3 years, 2018–2020, estimated from fetal growth (Y Matsuura, unpublished data)

distribution of birth periods among the northern Hokkaido population, estimated from fetal growth and assuming a gestation period of 224 days. In all 3 years, the peak occurred in mid-June, with 80% of the births completed during June. However, some individuals gave birth at the end of August. Two October births have been confirmed in captive populations in the Tokachi region of Hokkaido (Matsuura 2004); however, these neonates died within a few days of birth. In Hyogo and Kumamoto, the birth period was estimated to start in late April, with a peak in May (Koizumi et al. 2009). The latest births are estimated to occur in early September, and the range in birth period is as large as that in Hokkaido. Thus, despite peaks in the timing of conception and birth, late conceptions and births are sometimes observed. Late births are expected to be disadvantageous to newborn growth due to the shortened period before the winter season. The mortality rate of low-weight fawns has been reported to be higher in winter (Takatsuki and Matsuura 2000), and late births likely lead to higher mortality in winter. Also in red deer, neonates born later in the birth season have lower survival rates during winter (Clutton-Brock et al. 1982).

The causes of late births are related to delayed conception and prolonged gestation (Matsuura et al. 2004b). As mentioned above, gestation is prolonged in individuals in poor physical condition, such as low-weight females and young females in a severe winter. Age is also a factor in delayed conception. Suzuki et al. (1996) showed that the mean estimated conception date was significantly later for yearlings than for deer over 2 years of age. Observations of captive individuals have also revealed delayed conception among young females (Matsuura et al. 2004b). To summarize, harsh winters can cause both delayed conception and prolonged gestation in young females, which may explain the persistence of late births. The energy costs to females of gestation especially the last trimester (Pekins et al. 1998) and lactation (Clutton-Brock et al. 1982) are high, and therefore late births, which can lead to high winter mortality of fawn (Clutton-Brock et al. 1982), are seemed nonadaptive. However, late births may increase the chance of survival if the winter environment is favorable that year. In a study comparing the mortality rates of fawns in years with different winter snow cover, mortality rates were lower in years with less snow cover than in years with snow depths of ≥50 cm (Uno et al. 1998). Sika deer have very high mortality rates during the first year of life (Ueno et al. 2018), but a low mortality rate thereafter, such that late birth may not be a disadvantage for those deer that survive the first winter. Observations of captive deer also suggest that a birth delay of about 50 days has a small effect on subsequent growth (Matsuura 2004); therefore, it may be advantageous for sika deer to give birth if there is even a small chance that the newborn will survive.

7.6 Plural Corpora Lutea

Ovulation occurs during estrus, resulting in the formation of a corpus luteum in the ovary. The corpus luteum is present throughout gestation and plays an important role in producing progesterone, which is necessary for maintaining pregnancy. A single corpus luteum is usually formed in monogamous animals. However, although sika deer typically have only one newborn, plural corpora lutea have been found in 80.7% of individuals (Suzuki et al. 1992), usually in pairs, with three or four formed rarely (Fig. 7.2). Immunohistochemical staining of ovaries has clarified that the time of formation of plural corpora lutea is variable, whereas there was no variation in the ability to synthesize steroid hormones, suggesting that both corpora lutea produced progesterone (Matsuura et al. 2004c). Although plural corpora lutea have been found in other cervids with single fawn, such as red deer (Douglas 1966), elk (*Cervus Canadensis nelson*, Morrison 1960), and reindeer (Leader-Williams and Rosser 1983), their origin and role remain unclear. Two hypotheses have been proposed to explain the origin of plural corpora lutea: they may be a remnant of the estrous corpus luteum (Kelly et al. 1985) or newly formed after conception (Yamauchi et al. 1984). Yanagawa et al. (2015) later clarified the origin of second corpus luteum and

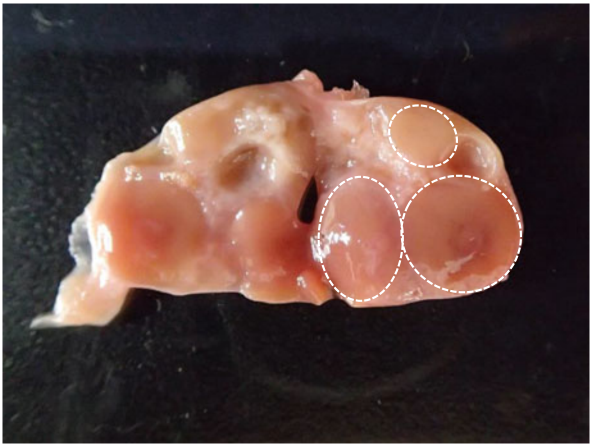

Fig. 7.2 Split section of sika deer ovary with three corpora lutea (dotted line)

inferred its role by observing the ovaries of captive animals at regular intervals before and after ovulation using ultrasound imaging equipment. The results showed that the second corpus luteum formed only in individuals that were conceived at the first estrus, whereas individuals that conceived at the second estrus had only one corpus luteum. The second corpus luteum was formed during a new ovulation event at 8–20 days after conception. Typically, postfertilization ovulation is suppressed by steroid hormone levels; however, these sika deer experienced postfertilization ovulation. Based on these results, the role of the second corpus luteum can be inferred as follows: when conception occurs at the first estrus, the progesterone concentration is low and insufficient to maintain pregnancy, such that a second corpus luteum is needed to synthesize supplemental progesterone. However, if conception occurs at the second estrus, sufficient progesterone concentration is easily produced by a single corpus luteum because the female has already been pre-sensitized to progesterone during her first estrus. Thus, it is likely that plural corpora lutea are part of a physiological mechanism that allows sika deer to maintain high fertility.

7.7 Ecological Significance

The high fecundity of sika deer, which causes high population growth, is maintained by several factors including the formation of plural corpora lutea. In livestock, such as caws and sheep, increased progesterone levels increase fetal survival, and plural corpora lutea is considered as a factor to increase progesterone levels (cows; Rajamahendran and Sianangama 1992; sheep; Shabankareh et al. 2012). Therefore, extra corpus luteum is artificially formed to increase progesterone level and reduce embryo mortality. In sika deer, plural corpora lutea are formed spontaneously, and those ensure the secretion of sufficient amounts of progesterone, which may result in lower fetal mortality. Pregnancy rates remain high throughout pregnancy periods in sika deer populations, such that abortion is rare. Prolonged gestation periods also contribute to catch up growth of fetus. When the fetal growth rate is low, such as in young or nutrition-poor females, the gestation period is prolonged to ensure sufficient growth occurs and increase the birth weight. Birth weight influences early mortality, with low birth weight inducing high mortality (e.g., red deer; Clutton-Brock et al. 1982). Prolonged gestation may lead to increased birth weight, thereby lowering the risk of early mortality in sika deer.

It is likely that a long birth period is promoting high fecundity in sika deer. Late births are not necessarily nonadaptive in this species, because the survival rate of late-birth fawns is not reduced under favorable winter conditions. Thus, the selection pressure against late births is weak. The reproductive strategy of sika deer appears to be based on conceiving and giving birth as frequently as possible, even if it results in late birth. On the other hand, there may be strong selection pressure on early births over late births. The frequency distribution of birth periods shows an asymmetrical pattern, with peaks skewed toward the first half of the period, tracking the pattern of simultaneous bud burst of plants in spring, followed by gradual withering in autumn

(Kikuzawa 1986). In spring, high-quality resources simultaneously become available to sika deer and slowly decline in quality over time until autumn. Therefore, mothers that give birth before the spring bud break will suffer from food shortages, increasing the mortality risk. In addition, extremely early birth is dangerous because newborn fawns are vulnerable to cold weather and food shortage. Therefore, extremely early births tend to be more disadvantageous than late births, which may explain the asymmetric frequency distribution of sika deer birth periods.

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Part II
Movements Ecology

Chapter 8
Movement Patterns of Sika Deer in Hokkaido Region

Yasuyuki Tachiki, Kohei Kobayashi, and Tsuyoshi Yoshida

Abstract GPS collaring surveys have increased since the early 2000s in Hokkaido. In this section, we reviewed the tracking data observed by more than 160 GPS collars worn in Hokkaido and discussed the movement pattern of deer throughout Hokkaido. The area with the longest seasonal migration distance was the Kushiro wetland (Takkobu area), which was 39.7 ± 23.3 (average ± *SD*) km. Further eastern areas such as Hamanaka (28.0 ± 17.8 km) and Hashirikotan area (22.7 ± 12.0 km) were areas with long distance movements. On the other hand, seasonal migration in the northern and western regions was shorter than that in the eastern Hokkaido; that average ranges from 10.2 to 14.6 km. The southern region is much shorter with an average of 6.6 ± 8.2 km. In areas where the migration distance is long, it can be said that it is necessary to cooperate in a wide area to take measures against deer. However, in areas where deer does not migrate seasonally, the deer population should be controlled at that location to prevent serious damage on local biodiversity. The results of the GPS collar survey give a significant suggestion to deer management in the Hokkaido area.

8.1 Introduction

In Hokkaido, the most northern island in Japan, the tracking of Yezo deer (*Cervus nippon yesoensis*; just mention "sika deer" in this chapter) via VHF telemetry has been conducted since the 1990s (Uno and Kaji 2000; Igota et al. 2009). GPS collars

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Y. Tachiki (✉)
Rakuno Gakuen University, SikaBase Japan, Ebetsu, Hokkaido, Japan
e-mail: y-tachiki@rakuno.ac.jp

K. Kobayashi
EnVision Conservation Office, SikaBase Japan, Sapporo, Hokkaido, Japan
e-mail: kobayashi@env.gr.jp

T. Yoshida
EnVision Conservation Office, SikaBase Japan, Sapporo, Hokkaido, Japan
e-mail: yoshida@env.gr.jp

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were introduced in a deer tracking survey in 2000, and today, GPS collars are applied throughout the whole area of Hokkaido. We estimate that more than 160 GPS collars (e.g., 106 in eastern, 16 in northern, 22 in western, and 18 in southern Hokkaido; Table 8.1) have been deployed by many organizations to track sika deer. A large number of deer have been tracked in the past, especially in the eastern part of Hokkaido, but deer tracking has also increased in the northern, central, and southern parts of Hokkaido in recent years. More than 100 years ago, in the 1870s, a large population of deer inhabited the entirety of the island of Hokkaido (Hokkaido Government 1987; Kaji et al. 2006), but this population decreased in number because of indiscriminate hunting and heavy snow in the late 1870s to 1880s (Hokkaido Government 1987; Kaji et al. 2006). Drastic changes in land use driven by humans from natural forests to agricultural fields are another major factor affecting this population decrease (Hokkaido Government 1987; Kaji et al. 2006). As a result of the protection policy established by the Hokkaido Prefecture government, the deer population has gradually increased since the 1980s in eastern Hokkaido. However, in the 1990s, the population rapidly increased not only in the eastern region but also in the northern and central regions (Kaji et al. 2000; Kaji 2003). With this increase in conflicts with the agriculture and forestry industries and with some parts of fishery production, traffic accidents and local biodiversity have become major issues. According to a report, the agricultural damage reached 3.8 billion yen (approx. 34 million USD) in Hokkaido in the year 2019 (Hokkaido Government 2019). There are many national parks and protection areas that contain unique and important biodiversity in Japan. For instance, 86% of wetlands in Japan exist in Hokkaido (Geospatial Information Authority of Japan 2000). The Shiretoko Peninsula, a world heritage site, is located in northeast Hokkaido. Now, it is necessary to plan countermeasures to control deer on behalf of related organizations such as the ministry, Hokkaido government, and municipality government. Background studies involving the tracking of many deer by GPS collaring have been conducted, as this is the first step to creating control strategies.

There is a small problem associated with the management of GPS collar data after a project has finished. Usually, data are preserved by the organization that has conducted the research but are separated into databases project-by-project, section-by-section, year-by-year, and organization-by-organization and are rarely shared among organizations. Sometimes, these data become difficult to find in the future, especially after the person in charge of the project has relocated. Therefore, we have tried to build a database, named "SikaBase," to gather GPS collar survey data (including data regarding where and when the project was conducted and by whom) to share mutually. SikaBase is a collaborative project including NGOs, private companies, and researchers who have deployed many GPS collars in Japan, and SikaBase is primarily focused on assisting decision-making by governments, municipalities, and local communities. In this paper, we would like to overview the movements of sika deer in many parts of Hokkaido using information that was gathered by SikaBase.

Table 8.1 List of GPS collars compiled by the SikaBase research group until 2019

Year	Project[a]	Place captured	Num. of collars[b]
2002	RP	Shiranuka town	5
2012	RP	STNP	9
2012	RP	Toyako Nakajima Island	3
2012	Simukappu Vill.	Shimukappu Vill.	3
2013	MoE	Hashirikotan	6
2013	MoE	Sarobetsu wetland	6
2013	JA Hamanaka	Hamanaka town, Kiritappu wetland	3
2013	MoE	KSNP	2
2013	RP	KSNP	1
2013	RP	KSNP	1
2013	RP	Sapporo city	1
2014	MoE	KSNP	10
2014	RP	KSNP	10
2014	RP	KSNP	9
2014	MoE	Sarobetsu wetland	6
2014	RP	Notsuke peninsula	4
2014	RP	Hamanaka town, Kiritappu wetland	3
2014	MoE	Hashirikotan	3
2014	FA	Hidaka area	2
2014	MoE	Lake Akan	2
2015	Hokkaido	Esan, Shiriuchi, Fukushima	15 (Inc. 3 male adults)
2015	Shiranuka town	Shiranuka town	6
2015	RP	KSNP	5
2015	MoE	Hashirikotan	4
2015	MoE	Lake Akan	4
2015	RP	KSNP	3
2015	RP	Notsuke peninsula	3
2015	FA	Tomakomai	3
2015	MoE	Sarobetsu wetland	2
2015	RP	KSNP	2
2015	RP	Shiretoko peninsula	2
2015	RP	Kiritappu wetland	1
2015	RP	KSNP	1
2015	EnVision	KSNP	4
2016	Shiranuka town	Shiranuka town	8
2016	HRFO	Yubari	2
2016	MoE	Lake Akan	1
2016	Hamanaka town	Hamanaka town, Kiritappu wetland	2
2018	FRMO	Lake Kussharo	3
2018	FA	Biratori town	2
2018	Hokkaido Pref.	Wakkanai	2
		Total	164

[a] RP: Research Project, MoE: Ministry of the Environment, FA: Forestry Agency, HRFO: Hokkaido Regional Forest Office, STNP: Shikotsu Toya National Park, KSNP: Kushiro

[b] Basically captured deer were female adults, except for annotation

8.2 GPS Collar Tracking in Hokkaido

The major GPS collar results obtained in Hokkaido are shown in Fig. 8.1. These results are listed by the SikaBase research group, with a total of 164 collars that were deployed from 2012 to 2019 (Table 8.1). These deer were all female adults except for three deer captured in southern part which were male adults. GPS-collared deer number may rise to approximately 200 when data from other research projects or from the latest project conducted by other organizations have been added.

As shown in Table 8.1, these results were obtained by projects that were conducted by the Ministry of the Environment, Forestry Agency, Hokkaido Prefecture government, universities, and the Japan Agricultural Cooperative. What is remarkable is that this large number of data points was obtained not by research institutes but by public administrations; this indicates the necessity of GPS collaring for public benefit. More detailed GPS collaring results in eastern, northern, central, and southern Hokkaido will be introduced in next sections. We used 134 GPS collar results on analysis and figures in following section that had been cleaned or permitted by copyright holder to be used before this moment.

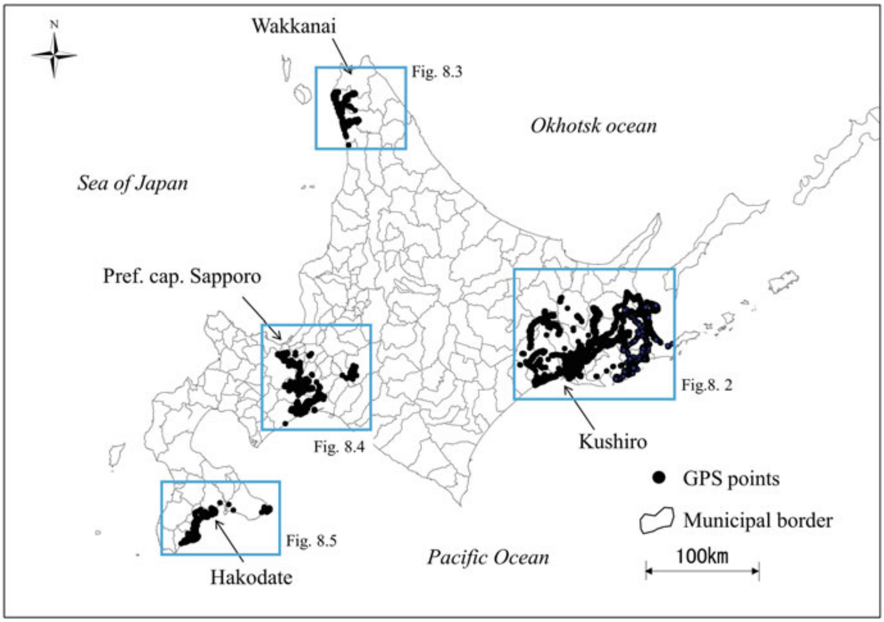

Fig. 8.1 Overview of the tracking of sika deer in Hokkaido from 2012 to 2019. Assembled by SikaBase group. Blue-colored square indicates section number and figure size in this chapter

8.3 Movement Patterns in Eastern Hokkaido

This area was known as traditionally high deer population area in Hokkaido. Before the year of 2000, deer conflict problem was limited in eastern Hokkaido, though it has been expanded in the whole area in Hokkaido today. It can be said that the history of deer management in Hokkaido had started here. This area contains many important places for local biodiversity conservation in Hokkaido, such as the Siretoko World Natural Heritage Site and Kushiro Shitsugen National Park (KSNP), which is the largest wetland in Japan; Kiritappu wetland, which is the third largest wetland in Japan; and the famous peninsulas Hashirikotan and Notsuke, which have unique ecosystems on sand spits. Therefore, eastern Hokkaido is one of the most important areas for the conservation of local biodiversity in Japan. The seasonal movements recorded in this area are shown in Fig. 8.2. For an easy-to-understand explanation, more details will be provided, starting from the southern region of this area (Shiranuka Hills) in an anticlockwise rotation to the northeast area (Shiretoko Peninsula) along the coastline.

Shiranuka Hills is the next town to the west of Kushiro City, where KSNP, the largest wetland in Japan, is located; Shiranuka Hills is connected to Akan-Mashu National Park in the north. These areas are comprised of sika deer that survive during the era of decreasing population (Kaji et al. 2006). For this reason, this region could be considered one of the most important "refuges" for sika deer. The Hokkaido government and Hokkaido Institute of Environmental Sciences have conducted tracking research on sika deer since the late 1990s; deer tracking was an advanced project in Japan at that time. The main target of the project was the group of deer that

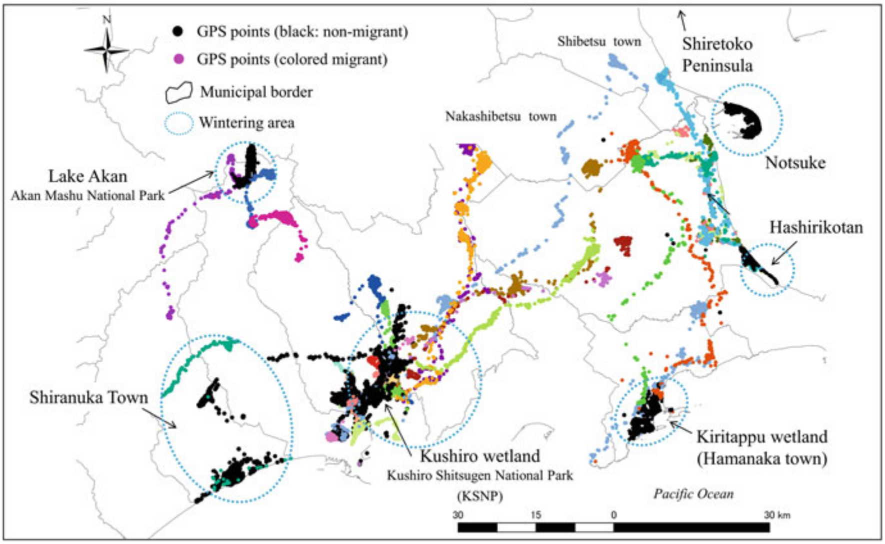

Fig. 8.2 Results of seasonal movements recorded in eastern Hokkaido

used a wintering place near Shiranuka Hills. Some groups of deer in this location (but not all) undergo seasonal migration, and one of the migration triggers in spring is snowmelt (characterized by snow depth) at the wintering place of the deer (Uno and Kaji 2000).

Sakuragi et al. (2003) verified that good food quality, such as pastures for daily farming, in the summer range of deer is one reason the deer who use Shiranuka Hills for wintering undergo seasonal migration. For migrating deer, the average distance of seasonal migration is introduced as 54 ± 30 km (average ± *SD*) in this paper. On the other hand, Igota et al. (2009) reported that they performed VHF telemetry tracking of 57 individuals in the same wintering place. According to that paper, 13 deer (approx. 22%) migrated to the east, 25 deer (approx. 44%) migrated to the north, and 12 deer (approx. 21%) did not migrate. The paper by Igota et al. mentioned that the average migration distance for migrants who used upward elevations for summer compared to the elevations of their wintering places was 58.7 ± 8.9 (average ± *SE*) km and that of migrants who used downward elevations in summer was 27.0 ± 2.3 km. The maximum seasonal migration distance was calculated as 101.7 km. The migration route of the deer also became clearer after the implementation of tracking; each individual deer used the same migration route when leaving and returning and moved quickly to their destination within only a few days. The summer home range size was 125 ± 25 (average ± *SE*)–123 ± 29 ha, which was generally larger than the winter range, determined to be 74 ± 19–107 ± 17 ha. These studies suggested many fundamental bases for planning deer management in Hokkaido that were subsequently carried out.

The Kushiro wetland is located in KSNP, next to the eastern area of Shiranuka Hills, and is known as the largest wetland in Japan according to the first Ramsar Conservation registered in 1980. A few deer that were captured and GPS collared at the Shiranuka Hills site mentioned above have used the northern edge of the wetland as their summer range, but only a small amount of information was known regarding the movement patterns of these deer until approximately 2012. Muramatsu and Fujita (2015) pointed out that a large population of deer use the embankments of the Shin-Kushiro River, affecting the high, moor vegetation in the Kushiro wetland. Two deer were captured and tracked by the deer population control project in Takkobu Lake by the Ministry of the Environment in the winter of 2013. One of the two captured deer used the (wintering) area during the summer season, but the other deer revealed a drastic result. The deer migrated more than 60 km northeast toward Sibetsu town, which is known as a giant pasture area, for its summer range. Although it should be noted that this result was based on only two deer, it indicated that the Kushiro wetland was one of the safe shelters in the hunting season for deer whose summer range was the Konsen plain field (famous for broad pasture farms). In addition, a new project funded by the Environmental Research and Development Fund (4–1405) of the Ministry of the Environment started in 2014. In this project, 15 GPS collars were deployed to female adult deer in KSNP at the right-side embankment of the Shin-Kushiro River in autumn but not in winter (approximately January to March). As a result, almost all deer who had used the right-side embankment (in KSNP) in summer used the inside of KSNP for wintering. Only a few deer left KSNP, but one was shot by hunter and another moved to an urban area in winter. The deer changed their habitats seasonally but did not travel as far distances (5.7 ± 1.3 (average ± *SE*) km) as those measured in previous research (Hino et al. 2017). It could be discussed that the hunting pressure for population control around the national park (protected area) is not efficient for deer who use only the inside of KSNP. The Ministry of the Environment changed their population control strategies based on this fact and started capturing deer inside of the wetland. Further, additional research conducted in Takkobu Lake in the wintering season showed that almost half of the deer migrated to the eastern broad pasture area in summer. The migration distance of these deer was 41.6 ± 11 (average ± *SE*) km (Hino et al. 2017).

Kiritappu Wetland, the third largest wetland in Japan, is located in Hamanaka town, on the eastern side of the Kushiro wetland. This area is famous for its dairy farming and fishing industries. The town office started a collaborative research project with Rakuno Gakuen University in 2013 and applied three GPS collars to female adult deer in the wintering season. After this project, another five collars were deployed in the same area; a total of 8 individuals had been tracked finally. According to the results, these deer used Betsukai and Nakashibetsu towns in summer and returned to the Kiritappu wetland in approximately November. Similar to the Kushiro wetland situation, it can be said that the studied deer use the Kiritappu wetland, a protected area for wildlife, as a “safe zone” during the hunting season. Another tracking research project was conducted in an area farther east. There are several unique sand spit landscapes along the Okhotsk coastline. One of these landscapes is called Hashirikotan. It is known that a large number of deer accumulate in the Hashirikotan wildlife reserve during the wintering season. According to observations conducted by helicopter, a total of 1333 heads were confirmed within the peninsula approx. 16 km^2 in winter (Ministry of the Environment 2016). In this area, 13 female adult deer were tracked by GPS collars. Most of these deer moved to pasture areas in Betsukai, Nakashibetsu, during the summer season. In this area, famous for farming and dairy products, 3.7 hundred million yen of agricultural damage by deer has been reported for 1 year (Hokkaido Government 2019). A large picture of the mechanism of the agricultural damage conducted in the far eastern Hokkaido area by deer can be obtained by gathering GPS collar data on the seasonal migration of deer in this large area.

While many deer have exhibited seasonal migration in some areas, such as the KSNP, nonmigrating (resident) groups were confirmed in another area in eastern Hokkaido. The Notsuke Peninsula is a sand spit that is just into the Okhotsk Sea, located next to Betsukai town; this is a highly agriculturally damaged area, as mentioned above. The Notsuke Peninsula has a unique and beautiful landscape and serves as an important habitat for many migrating birds and natural Sakhalin fir (*Abies sachalinensis*) stands that are developed on sandbars in sea-level marshes. As this area is also a wildlife protection area, it is known that a large number of deer use this area as a wintering place and damage the beach vegetation. Four female adult deer were tracked by GPS collars to their Notsuke Peninsula wintering place because people thought these deer must be moving to the mainland during the summer season and damaging pastures or crops in Betsukai town. However, surprisingly, no tracked deer left the peninsula throughout the year. Recently, beach vegetation, such as Ramanas rose (*Rosa rugosa*), was shown to be heavily grazed by deer. The results of this project indicated that deer management strategies, such as population control, are needed and should be conducted inside of the peninsula to protect its sensitive ecosystem.

The Shiretoko Peninsula, a world natural heritage site, is located at the northeast edge of Hokkaido Island. For appropriate ecosystem management, deer management, such as population control, has been conducted by the Ministry of the Environment, Forestry Agency, and Shiretoko Nature Foundation in this region. To develop an effective deer management strategy, 20 GPS collars were deployed on deer on this peninsula (Ministry of the Environment 2015; Ministry of the Environment 2016; Ishinazaka 2013). The data from GPS collars showed that most deer did not leave the peninsula, but some of the deer moved to higher altitudes and returned to the lower coastline seasonally (Ishinazaka 2013), while others stayed at the same place in all seasons. For instance, the home ranges over 1 year were very limited, measured at only 0.7–2.9 km^2, for ten deer who were tracked from Rusha, located on the north coastline of the peninsula (Ministry of the Environment 2015. However, in the second year of tracking, one deer suddenly migrated to the other (south) side of the coastline. Another deer who was newly investigated in August 2016 also migrated seasonally from the north to south coastlines. Although some deer undergo seasonal migrations, as pointed out above, it can be said that the habitat ranges of most deer in the Shiretoko Peninsula are generally much smaller than those in other studied areas (Ministry of the Environment 2016). Different weather conditions on the northern and southern sides of the peninsula in winter affect the movement patterns of deer. All these results provide meaningful information for deer management strategies on the Shiretoko Peninsula (Ishinazaka 2013).

All results mentioned above were obtained along the coastline of eastern Hokkaido. Next, we focus on the central area of eastern Hokkaido. Except for the eastern coastline of the lake, the main part and upper stream forest of this lake belongs to private land that is managed by the Maeda Ippoen Foundation. This foundation contributes greatly to local biodiversity conservation, such as conservation of the moss balls, by not only forestry or stream management but also by deer population control measures, as deer damage the forest in the area. Akan Lake is located more than 400 m above sea level and has heavy snow in winter. The directions of migration to reach the summer ranges of the deer were north and south (for the north edge of the Kushiro wetland), and the confirmed nonmigrating group was the same as that in another wintering area. Uno and Kaji (2000) conducted VHF telemetry tracking in this area. They reported that the distances of the seasonal migrations were, in the case of migration from the winter to summer ranges, 19.9 ± 13.0 (average ± *SD*) km and, in the case of migration from the summer to winter ranges, 24.3 ± 13.2 km (Uno and Kaji 2000). In addition, the Ministry of the Environment has started tracking deer at the Kussharo Lake, which is located next to the eastern side of Akan Lake and is included in the same national park (Akan Mashu National Park), for deer management planning in these locations.

8.4 Movement Patterns in Northern Hokkaido

Hokkaido is the island in Japan with the highest latitude, and the most northern area in Hokkaido is over 45 degrees north. The west coast of northern Hokkaido faces the Sea of Japan, which has heavy snow weather in winter with very strong winds from the northwest that cause blizzards to be frequent. We may think this winter condition is not a suitable habitat for deer, but deer fit this harsh environment by the optimal use of terrain and vegetation as barriers. Compared with eastern Hokkaido, deer population expansions are delayed in this region (Inatomi et al. 2015; Hokkaido Government 2019); however, agricultural damages have gradually increased in this area since the early 2000s. Movement pattern of deer in this region, as tracked by GPS collars, is shown in Fig. 8.3.

Wakkanai City is a hub of this area and is located at the northern tip of Hokkaido Island. The largest high moor exists approximately 30 km south of Wakkanai city, named the Sarobetsu wetland. This wetland is famous not only as a transit point for migrating birds but also for the Wakasakanai dune forest, which stretches along the coastline and contains natural Sakhalin fir and Sakhalin spruce (*Picea glehnii*) stands. This area belongs to Rishiri-Rebun-Sarobetsu National Park. As the Ministry of the Environment and Forestry Agency recently reported, vegetation damage in the national park has been recently confirmed, as nine female adult deer were captured in the wintering season and traced by the GPS collar in 2015 and 2016 in the Sarobetsu wetland. Deer groups that were captured at the Teshio River mouth were moved inland, and some of the deer that were captured in the Toyotomi area migrated more than 10 km to the northeast, crossing wetlands, and used pasture areas for their

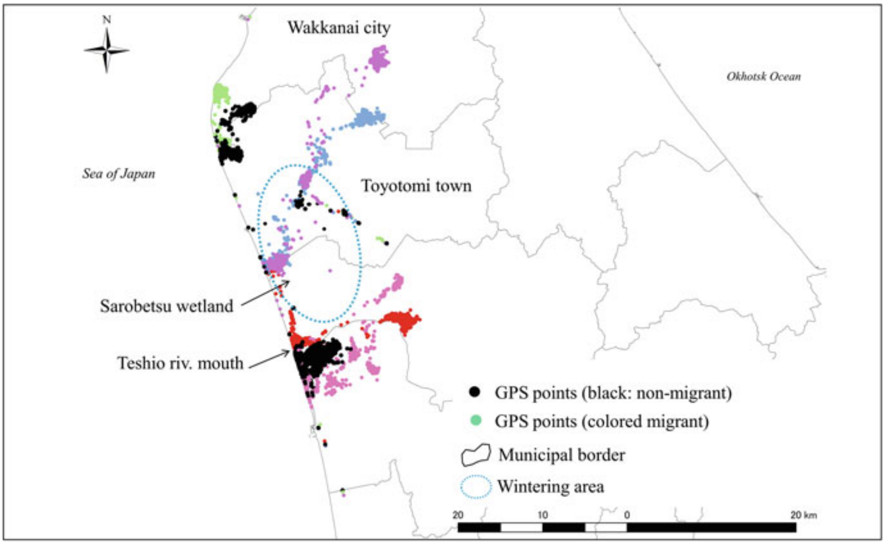

Fig. 8.3 Results of seasonal movements in northern Hokkaido

summer ranges. The key industry of Toyotomi town is dairy farming. Similar to what was seen in eastern Hokkaido, the summer habitats of the tracked deer were nearby large pasture lands.

Long seasonal migrations, such as those observed in eastern Hokkaido, have not yet been confirmed in this region. However, many deer have been observed to form lines and walk somewhere in the early March snowmelt season, but nobody has determined where these deer were migrating, as a very limited number of GPS collaring surveys have been conducted in this area. If we have the chance in the future, we wish to conduct GPS collar research this area.

8.5 Movement Patterns in Western Hokkaido

This area is located west of the Hidaka Mountain range, in which Hokkaido is like a spine, and is east of Shikotsu Toya National Park, facing the Japan Sea to the north and the Pacific Ocean to the south (Fig. 8.4). This area contains Hokkaido's largest city, Sapporo, the so-called economic and urbanization center of Hokkaido, with a high population and high human density. The Hokkaido government recently reported that deer population size indices, such as spotlight counts conducted by the Hokkaido government and Hunting Association, are recently receiving higher values in some areas of this region than those in eastern Hokkaido (Inatomi et al. 2015; Chap. 32). For instance, some coastal areas of the Pacific Ocean, such as Hidaka town, produce racehorses, and it is difficult to use guns near thoroughbred

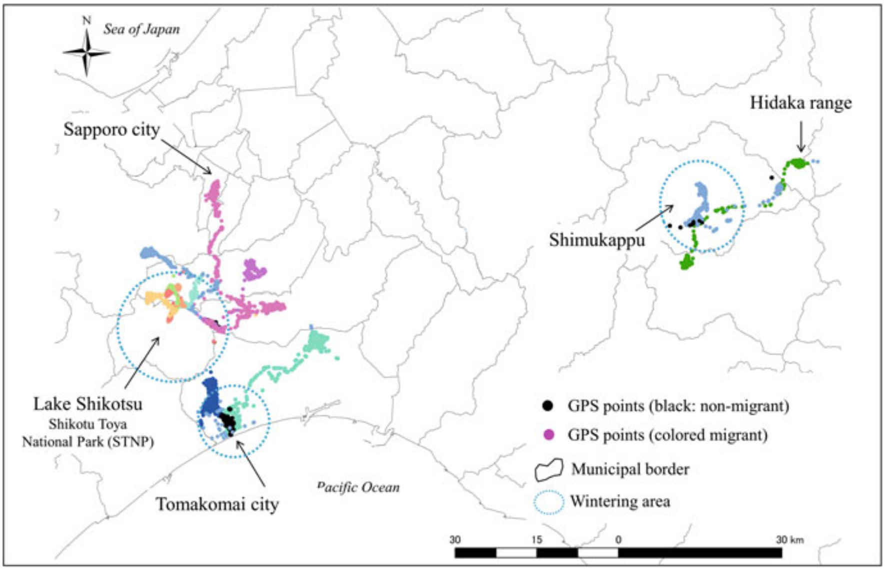

Fig. 8.4 Results of seasonal movements in western Hokkaido

stables because of gun sounds. In addition, the natural mortality rate is not high because the snow depth in winter is not deep in many areas, such as on the northern coastline. These complex situations make this area the “center of explosion” of the deer population in western Hokkaido. Figure 8.4 shows the results of the seasonal movements of deer in western Hokkaido.

Sapporo is the fifth largest city in Japan, and nearly two million citizens live there. Recently, the so-called urban deer problem (Tachiki 2015; Honda et al. 2018) has become a major issue in this city. These deer suddenly appear in urban areas and cause panic for urbanized people. This urban deer problem has been managed by the Sapporo City government since 2012. While managing projects, they have also tried to determine the route of the deer “invasion” into urban areas and their seasonal movements from surrounding forest areas (Sapporo City Government 2011; Tachiki 2015). For this reason, two male deer were captured in the southern area of Sapporo City and traced by GPS collars in autumn 2013. These two deer underwent seasonal migration approximately 30 km to the south, near Shikotsu Lake, to winter. This was the first deer tracking project in the Sapporo area. In the winter of the same year, another large research project was conducted by tracking nine female deer at Shikotsu Lake. Two of the nine deer (approx. 22%) migrated 10–20 km to the north and used Sapporo City area for their summer habitat, while six of the nine deer (approx. 67%) migrated less than 20 km to the north and did not use Sapporo City but instead used a nearby city for their summer range; one of the nine deer did not migrate. By overviewing these results, it can be concluded that Shikotsu Lake is one of the sources of Sapporo’s urban deer. This lake is included in Shikotsu-Toya National Park. A similar situation as those seen in eastern and northern Hokkaido can be seen in this area. Although the deer population is increasing in the south coastline area, few deer have been studied in this area until now. Two adult female deer in the Hidaka region and three adult female deer in Tomakomai were captured and tracked by GPS from 2015 to 2016, but these deer did not migrate as far as the Shikotsu Lake deer. When these results were revealed, we thought that long-distance migration is not a feature of deer behavior in this area. However, one adult female deer traced in 2019 from Biratori town migrated to the Hidaka range in the summer season (Forestry Agency Hokkaido Regional Forest Office 2019). This was the first record in this area and indicated the possibility that some deer that damage highland vegetation in the Hidaka range come from the Pacific coast area.

8.6 Movement Patterns in Southern Hokkaido

The southern part of Hokkaido that will be focused on in this section roughly includes all southwest areas of west Hokkaido that were mentioned above. The deer population size in this area has been quite low in the past (Hokkaido Government 2017; Chap. 32). However, the deer habitat has recently expanded, and agricultural damages and hunting reports are now increasing in this area (Hokkaido Government 2017, 2019). Furthermore, it is known that the deer populations are

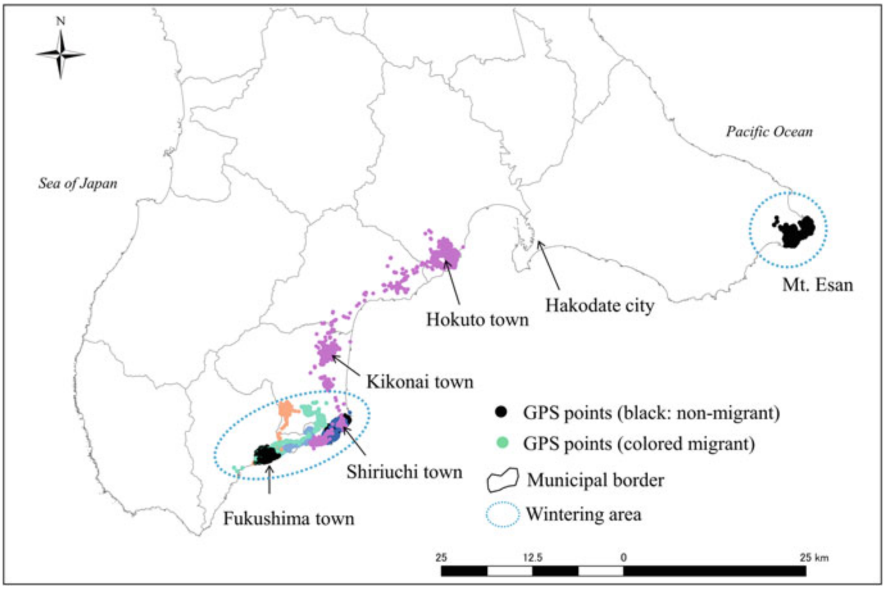

Fig. 8.5 Results of seasonal movements in southern Hokkaido

rapidly increasing at limited points in this area, such as the Esan, Shiriuchi, and Fukushima areas, which are located at the southern tip of Hokkaido (Hokkaido Government 2016), and vegetation damage is a concern in these regions. Because of this background, the Hokkaido government conducted a tracking project of 15 adult deer (12 females, 3 males) in this area in 2015 to determine the deer population and their movement patterns in the southern area of Hokkaido. An outline of the results is shown in Fig. 8.5.

According to the results, a total of five deer had migrated. The most longest distance travelled one (female) was captured in the Shiriuchi area migrated 28 km to the northeast to a point called Kikonai town and Hokuto city for its summer range. Another one female deer that was captured in the Fukushima area moved 7 km to the northeast and spent the summer there. Other three deer (two females, one male) were qualified as “migrated” because their summer and winter range was not overwrapped, but the distance between each range was quite near, only few kilometer. These five deer underwent seasonal migrations, but these migrations were not over long distances, such as those observed in eastern Hokkaido. The other ten deer (eight females, two males) were nonmigrat. As an overview of these results, most deer in southern Hokkaido do not migrate long distances like deer in other areas.

8.7 Conclusion

As the deer population has remarkably increased since the 1990s in Hokkaido, many advanced ecological studies have since been conducted on deer (Uno and Kaji 2000; Sakuragi et al. 2003; Igota et al. 2004; Hino et al. 2017). We consider the background reasons for this to be as follows: Hokkaido Island is the largest island in Japan and belongs to one prefecture; second, advanced GIS databases and technologies have been developed since the 1990s; and third, Hokkaido is good for GPS positioning because, compared to other areas in Japan such as Honshu (main) Island, the topography in Hokkaido is not as hilly and the forest canopy is not as dense. Thanks to previous efforts to deploy more than 160 GPS collars to collect data, the movement patterns of deer have become clearer than before.

In this chapter, the tracking results were shown along the coastline from the eastern to the northern, western, and southern areas of Hokkaido. The summary of the GPS collaring result that mentioned in this chapter is shown on Table 8.2. The migration distance on Table 8.2 was calculated by measuring the longest side of the GPS point-to-point distance in kilometer by GIS. As shown in Table 8.2, the longest seasonal migration distance was Kushiro wetland (Takkobu area) that was 39.7 ± 23.3 (average ± *SD*) km. Other eastern Hokkaido area such as Hamanaka and Hashirikotan area also has longer migration distance as 28.0 ± 17.8 km and 22.7 ± 12.0 km. It can be said that deer in eastern Hokkaido area tend to migrate more longer distance than other area in Hokkaido.

Migration rate (migrant vs. nonmigrant) was also high value in similar area. For instance, the highest in the eastern area was in Takkobu (11/12, 91.7%), and second highest in this area was in Hashirikotan (migrant 9/13, 69.2%). On the other hand, in eastern Hokkaido lower migrant rate values were seen in Shiranuka (1/14, 7.1%) and in Notsuke Peninsula (1/7, 14.2%). It can be said that migrant vs. nonmigrant rate affected their character of particular habitat use pattern. The average migration distance in northern and western Hokkaido ranges from 10.2 to 14.6 km in average. Furthermore, in southern area, it is much shorter than other area in average such as 6.6 ± 8.2 (average ± *SD*). These data provide important suggestions for deer management planning that are necessary for the conservation governance of deer in Hokkaido. For instance, in areas where there are many deer migrating long distances, it can be said that it is necessary to collaborate with surrounding municipalities to counter against deer. The Ministry of the Environment has started planning deer management in Kushiro Shitsugen National Park; the next population control operation will be planned based on GPS collar data. On the other hand, in the area where deer did not conduct seasonal migration or not long-distance movement in whole year, it will be necessary to concentrate deer management at those areas such as Mt. Esan, southern part of Hokkaido. In fact, capturing by corral trap project by Hokkaido government had been done in this area based on GPS collaring survey.

A map that shows GPS collar data is very easy for anyone to understand. Therefore, it can be a useful item to involve various stakeholders in deer management in that area. And also, it is effective to design a big picture of deer management

Table 8.2 Number of GPS collars in this chapter and summary of migration in each area of Hokkaido

Area of Hokkaido	Eastern								Northern	Western		Southern
		KSNP[a]									STNP[b]	
Place	Shiranuka	Kushir Riv. Embarkment	Takkobu	Kottaro	Hamanaka, Kiritappu wetland	Hashiri-kotan	Notsuke peninsula	Lake Akan	Sarobetsu wetland	Tomakomai, Shimukappu, Biratori	Lake Shikotsu	Esan, Shiriuchi
GPS collars[c]	14	15	12	12	8	13	7	7	13	7	9	15
Migrate	1	9	11	3	4	9	1	4	10	5	8	5
Nonmigrate	13	6	1	9	4	4	6	3	3	2	1	10
Migration distance (km)												
Average	6.3	9.0	39.7	18.3	28.0	22.7	7.9	9.4	14.6	17.7	10.2	6.6
SD	6.3	3.2	23.3	10.7	17.8	12.0	0.9	2.4	8.9	10.0	7.4	8.2
Max.	25	15	78	45	50	43	9	12	30	30	27	34
Min.	2	5	5	5	3	2	7	6	1	5	3	2

a1KSNP: Kushiro Shitsugen National Park

b2STNP: Shikotsu Toya National Park

c3Number of GPS collars that were used in this chapter in certain area to do correct plan-do-check-action cycle. The SikaBase research group will continue gathering GPS collar information before it disappears and wishes that these data will not only be used by ecological researchers but also return to local residents as a benefit for practices such as effective management.

Acknowledgments This manuscript was written in collaboration with many organizations. We would like to thank the Ministry of the Environment, Forestry Agency Hokkaido Regional Forest Office, Hokkaido government, JA Hamanaka, Betsukai town, and EnVision Conservation Office who shared GPS collar data. We also thank Ms. Tomomi Kudo and Dr. Rika Akamatsu who gave great support to sort out GPS data. Thank you very much.

Each GPS collar data is very important. These data are the fruits of all people's great efforts, including all projects, and by good luck, the deer survived during the tracking term and the GPS collars did not break until the data were retrieved. We would like to pay respect to all the people included in the projects from which we have introduced results in this chapter.

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Chapter 9

Movement Patterns of Sika Deer in Tohoku Region

Kiyoshi Yamauchi, Takeharu Uno, Takuya Kinota, and Shunpei Tasaki

Abstract Until approximately 100 years ago, sika deer (*Cervus nippon centralis*) were widespread in the Tohoku region of northeastern Honshu, Japan. However, heavy snowfalls and high hunting pressure restricted their distribution to a narrow area along the coast of the Pacific Ocean. The population began to increase again in the 1980s, and the distribution of this species has expanded rapidly since 2000. Such a decline and subsequent recovery in the sika deer population are characteristic especially in northern Japan. In this chapter, we review the differences in the behavior of sika deer in areas with high sika deer population densities along the coast and newly settled areas using tracking data obtained using GPS collars. In addition, we describe the adaptive behavior of deer in coastal areas where the environment was altered dramatically by the Great East Japan Earthquake in 2011.

9.1 Introduction

9.1.1 History and Distribution of Sika Deer in the Tohoku Region

Ancient documents show that from the Jomon period to middle the Edo era, sika deer were widespread in the Tohoku region (Tsujino et al. 2010), with a distribution that extended from the coast to inland areas (Endo 1994; Mori and Tadano 1997; Mutou 2017). From the end of the Edo era to the Meiji era, advances in firearms and their increased availability among the public resulted in a marked decline in the sika deer population in the region (Takatsuki 1992a). From the Taisho era to the early Showa era (from 1919 to 1929), hunting was banned, but overhunting occurred in the

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K. Yamauchi (✉)
Faculty of Agriculture, Iwate University, Morioka, Japan
e-mail: yamaky@iwate-u.ac.jp

T. Uno · T. Kinota · S. Tasaki
Tohoku Monkey and Mammal Management Center, Sendai, Miyagi, Japan
e-mail: uno@four-m.jp; kinota@four-m.jp; tasaki@four-m.jp

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chaotic period that followed World War II. In Hokkaido, severe winters with heavy snowfalls resulted in an increase in the number of deer deaths (Tawara 1979), and it seemed that similar heavy snowfalls occurred frequently in the Tohoku region. The combined effect of human activities and heavy snowfalls resulted in regional extinction of sika deer, with populations becoming restricted to the area around Mt. Goyo in Iwate Prefecture and Kinkazan Island and Oshika Peninsula in Miyagi Prefecture.

In an attempt to restore the size of the sika deer population, a variety of measures were implemented in the region. These included a ban on hunting female sika deer in 1949, the establishment of a wildlife refuge in 1948, and a ban on the use of hunting dogs in 1955 (Takatsuki 1992a). At the same time, a revolution in fuel occurred as firewood and charcoal were replaced by fossil fuels, such as oil and natural gas. As a result, afforestation with conifers increased rapidly and coppice forests decreased. Some forested areas were also partially converted to open spaces such as grasslands, which provided convenient feeding grounds for sika deer (Iijima 2018). In the 1970s, the development of large-scale grass farming and pasturelands in the Kitakami Highland Mountains (Ajisaka 1970; Nasuno 1982; Komatsu 1983; Mino et al. 2010) also had the effect of increasing food resources and greatly altered the habitat of sika deer. Taken together, these changes had a marked effect on the population dynamics of sika deer in the region. Since the 1980s, the number of animals shot by sport hunters has increased steadily, and culling in response to agriculture and forestry damage has also gradually been implemented. In the late 1980s, damage attributed to sika deer increased rapidly, and the number of sika deer that were hunted and culled annually almost reached 2000 (Iwate Prefecture 2002). Most of the damage was caused by sika deer feeding on nursery trees in afforested areas and on crops in areas around human settlements. Iwate Prefecture established a committee to assess the damage caused by sika deer in 1994 and began to conduct habitat and environmental surveys around Mt. Goyo. Initially, the planned initiatives were intended to protect sika deer populations. However, as the distribution of sika deer extended into the areas surrounding Mt. Goyo, the planned initiatives shifted to control of the population size once the Wildlife Protection and Proper Hunting Law was amended in 1999. The rapid decrease in the number of hunters that has occurred in recent years, combined with the decrease in human activity in mountainous areas, has resulted in a lack of maintenance of the woodland areas near villages and an increase in abandoned agricultural areas. Together, these factors have contributed to a marked increase in the sika deer populations in the region (Chap. 2). This expansion in the distribution of sika deer has resulted in an increase in crop damage and increased sightings of sika deer, not only in Iwate Prefecture, but also in the neighboring prefectures of Akita and Aomori. In addition, similar increases in deer populations and distribution have occurred throughout Japan. Subsidies from the Ministry of Agriculture, Forestry, and Fisheries have been introduced to promote large-scale culling of sika deer and to prevent damage to crops and forests from 2008.

The Great East Japan Earthquake, which occurred on March 11, 2011, also affected the distribution of sika deer. A tsunami hit the coastal areas of the Tohoku region where sika deer were densely distributed, causing considerable damage to the region. The release of radioactive cesium from the Fukushima Daiichi Nuclear Power Plant accident resulted in cesium being detected in the muscles of wild birds and animals, and the sale of wild meat was prohibited. As the motivation of hunting decreased, so too did the number of animals that were hunted. Iwate Prefecture has therefore introduced financial incentives to hunt deer. Moreover, a certification system for professional culling was introduced after an amendment to the Wildlife Protection and Proper Hunting Law in 2014. Promulgation of the law has resulted in more than 10,000 sika deer being culled annually.

9.1.2 Purpose

While the populations of sika deer in the northern Japan have experienced extirpation, population recovery, and rapid range expansion (Kaji et al. 2000; Uno et al. 2009), other regions of Japan have not experienced these phenomena. It is therefore considered likely that the behavioral patterns of sika deer in the Tohoku region differ from those in other regions. In recent years, financial incentives for culling have been introduced, and the number of culled animals has increased in the coastal areas where sika deer are present at high densities. Recently, the population densities of sika deer in the areas outside the coastal region have increased to levels that exceed those in the coastal areas, and structural changes in the distribution of sika deer populations in the Tohoku region have been observed. Furthermore, changes in sika deer behavior also occurred due to the Great East Japan Earthquake, primarily in response to the large-scale construction projects that followed the disaster. For example, residential areas have been relocated to higher-lying areas, and the areas between mountains have been developed. Two telemetry surveys were conducted previously in the Tohoku region. From the late 1980s to the early 1990s, when sika deer were restricted to the area around Mt. Goyo, behavioral surveys using radiotelemetry were conducted (Takatsuki et al. 2000). That study reported that several individuals showed migratory behavior in response to snow cover, but that the distances migrated were relatively short. From 2004 to 2005, when the distribution of sika deer began to expand, a GPS collar telemetry survey was conducted at a site where severe crop damage occurred in the foothills of Mt. Goyo (Wildlife Management Office 2006). Although only two out of the five animals migrated 2 or 3 km from areas surrounding human settlements to higher-altitude areas during the winter, both individuals remained in a nearby pasture; this behavior was clearly due to the presence of food resources.

In projects undertaken by the Forestry Agency and Tohoku Regional Forest Office to conserve rare plants in the national and quasi-national parks, and/or in projects undertaken by Kamaishi City to prevent deer from entering urban areas, behavioral tracking surveys of sika deer using GPS collar telemetry have been conducted from 2014 to 2020. The GPS location information used in these surveys is considerably more accurate than that obtained by the radiotelemetry surveys used in the past. In this chapter, the results of the GPS collar telemetry surveys are summarized, and the behavioral patterns of sika deer in the Tohoku region are reviewed. Seasonal migration and the timing of migration were also considered; in particular, the relationship between the winter home range and snow depth was analyzed because heavy snowfall occurs in the Tohoku region.

9.2 Methods

9.2.1 Topography and Climate of the Tohoku Region

The Tohoku region is located in the northernmost part of Honshu and consists of the six prefectures of Aomori, Iwate, Akita, Miyagi, Yamagata, and Fukushima (Fig. 9.1). The Ou Mountains run north and south through the center of the region, and the Dewa Mountains and the Kitakami Highlands rise in parallel to the west and east, respectively. Large rivers, such as the Mogami River and the Kitakami River, flow through the mountains and into estuaries on the Shonai Plain and the Sendai Plain, respectively. There are many mountains in the Tohoku region, which also contains the Kitakami Basin, the Yamagata Basin, and the Aizu Basin, all of which are densely inhabited. The Sanriku Coast, which lies to the east of the Kitakami

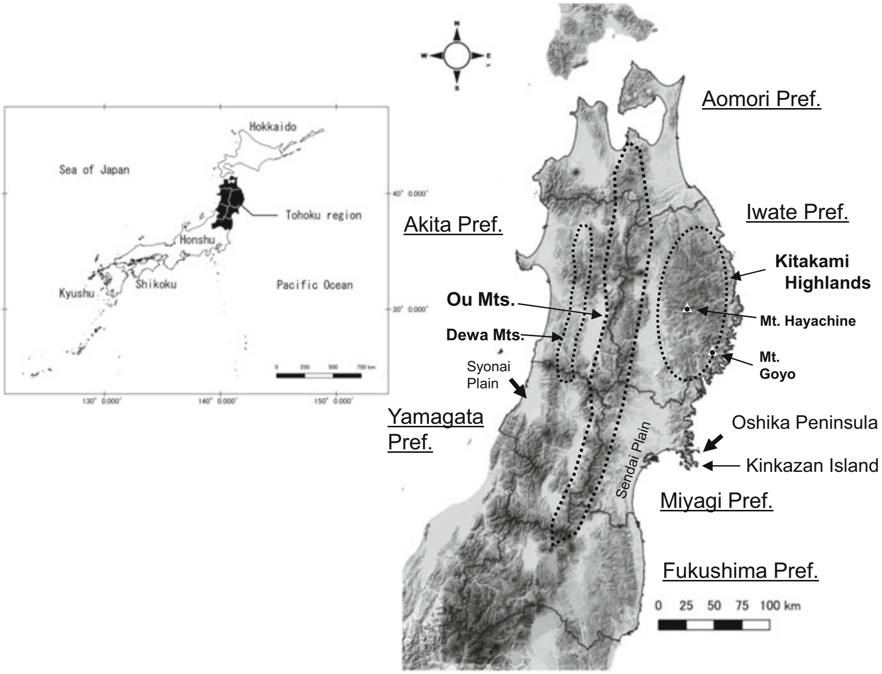

Fig. 9.1 Map of the Tohoku region, Japan

Highlands, is a “rias coast” and is characterized by being highly irregular with numerous bays.

The Tohoku region is located at a high latitude, which means that the temperature is lower than in other parts of Honshu. The area is longest from north to south, and the average temperature difference between the north and the south is about 3 °C to 4 °C. There are differences in snowfall and rainfall between the Pacific Ocean and Sea of Japan sides. On the Pacific Ocean side, the Chishima Current causes moist winds during the summer called “Yamase,” and these are associated with fog and cool weather. Indeed, sometimes summer temperatures in this region do not rise.

In winter, cold air from Siberia is transported into the Tohoku region. When the air crosses the Sea of Japan, it absorbs moisture and forms snow when it hits the Ou Mountains. Consequently, heavy snowfalls are common along the Sea of Japan coast and inland mountains. Once this cold air loses its moisture, the dry air moves toward the Pacific Ocean, which explains the marked differences between the Pacific Ocean and Sea of Japan sides of the Ou Mountains. In some years, there is very little snowfall on the Pacific Ocean side of the region.

At 1917 meters above sea level (a.s.l.), Mt. Hayachine in Iwate Prefecture is the highest peak in the Kitakami Highlands. The mountain supports numerous rare and endemic plant species, and the area around Mt. Hayachine, including the nearby Mt. Yakushi and Mt. Keito, has been designated as a quasi-national park. In response to damage due to bark-stripping and bite marks on branches and leaves by sika deer over the last 10 years, concern has increased regarding the decline in the multifunctional roles of forests as well as the risk of damage to rare alpine plant species.

Mt. Goyo is located in the southern part of the Kitakami Highlands on the Pacific Ocean side of the Tohoku region. At 1351 meters a.s.l., it is the second highest mountain in the Kitakami Highlands after Mt. Hayachine. During the feudal era, Mt. Goyo was protected by the Date Clan, and the number of people that were allowed to enter the area was highly restricted. At present, the entire Mt. Goyo area is a designated Prefectural Natural Park and Wildlife Protection Area. Kinkasan Island is a small island (960 ha) located south of Mt. Goyo. The island is a shrine sanctuary, and sika deer are protected there. It is considered that sika deer have inhabited the island without being extirpated as there is little snowfall and conservation measures (hunting bans) have been implemented in these coastal areas, including the Oshika Peninsula.

The following observational data were used for the analysis in this chapter. Data for the average daily snow depth from January to February during 2015 to 2019 were obtained from the closest meteorological observatory in each study region as there were no measurement records for each survey site. In the Hayachine and Tono regions, the data from the Kuzakai observatory (39°39.0′N, 141°21.2′E, 760 m a.s.l.) in Morioka City and the Tono observatory (39°20.2′N, 141°32.3′E, 273 m a.s.l.) in Tono City were used, respectively. The mean values were 50.9 cm and 6.1 cm in the Kuzakai and Tono regions, respectively. The data for the coastal region were obtained from the Ofunato observatory (39°3.8′N, 141°42.8′E, 37 m a.s.l.) in Ofunato City, and the mean value was 0.5 cm, indicating that the region experienced almost no snowfall. These meteorological data including temperatures were downloaded from the website of the Japan Meteorological Agency (2020). The meteorological data and the durations of the summer and winter home ranges of all individuals were overlaid. Elevation data was downloaded from the 10 m Digital Elevation Model of the Geospatial Information Authority of Japan (2019), and slope direction and slope data were obtained by processing this elevation data with Raster Analysis of QGIS (QGIS Development Team 2020).

9.2.2 *Deer Capture and Data Analysis*

The authors fitted 23 sika deer with GPS collars from 2014 to 2020 (TrackM2D, LOTEK, Ontario Newmarket, Canada; Lite Track IRIDIUM420, LOTEK; GLT-03, Circuit Design, Nagano, Japan; GPS-TX, Mathematical Assist Design Laboratory, Gunma, Japan) (Forestry Agency 2015; Kamaishi City 2017, 2018; Tohoku Regional Forest Office 2015, 2016a, b, 2017a, 2017b, 2017c, 2018, 2019, 2020). The devices were fitted to deer in the Hayachine region (12 animals) and Tono region (3 animals) in Iwate Prefecture, and the coastal region (8 animals) between Iwate and Miyagi prefectures. Figure 9.2 shows a map of each region and the locations where sika deer were captured.

Sika deer were captured using tranquilizer gun or leg-binding trap. The handling of captured individuals was in accordance with the Guidelines for the Procedure of Obtaining Mammal Specimens as Approved by the Mammal Society of Japan (Species name and Specimens Committee, The Mammal Society of Japan 2009). The weight of the GPS collar (transmitter) was <5% of the deer body weight in consideration of its possible effect on wildlife behavior (Macdonald and Amlaner 1980). Four sika deer in the Hayachine region that were fitted with GPS telemetry collars in 2014–2015 became untraceable within 2 months of the collars being fitted due to malfunctioning of the GPS devices. Therefore, these individuals were excluded from subsequent analyses. A total of 19 sika deer (8 animals in the Hayachine region, 3 animals in the Tono region, and 8 animals in the coastal region) were tracked for 161–1067 days (Table 9.1). The GPS collar was set to acquire the animals' location every 3 hours and, for only the KA-1 collar, every hour (Table 9.1). An analysis of the data obtained for these 19 sika deer (4 males and 15 females) is described in this chapter. In order to exclude data with low position-fix accuracies, only 3D fix data that received signals from four or more GPS satellites were used in the analysis. The definition of seasonal home range was based on that employed by Takii et al. (2012a). Briefly, summer and winter home ranges were defined as the area in which an individual remained for more than 30 days without moving more than 2 km in any direction in 1 day (Takii et al. 2012a). The home ranges of each year were plotted using the fixed kernel method (150 m radius, 90%) using the adehabitat package for R (Calenge 2006), and the areas of each home range were calculated. The center of activity in each year was calculated using the mean latitude and longitude (Hayne 1949). The distance (measured as a straight line

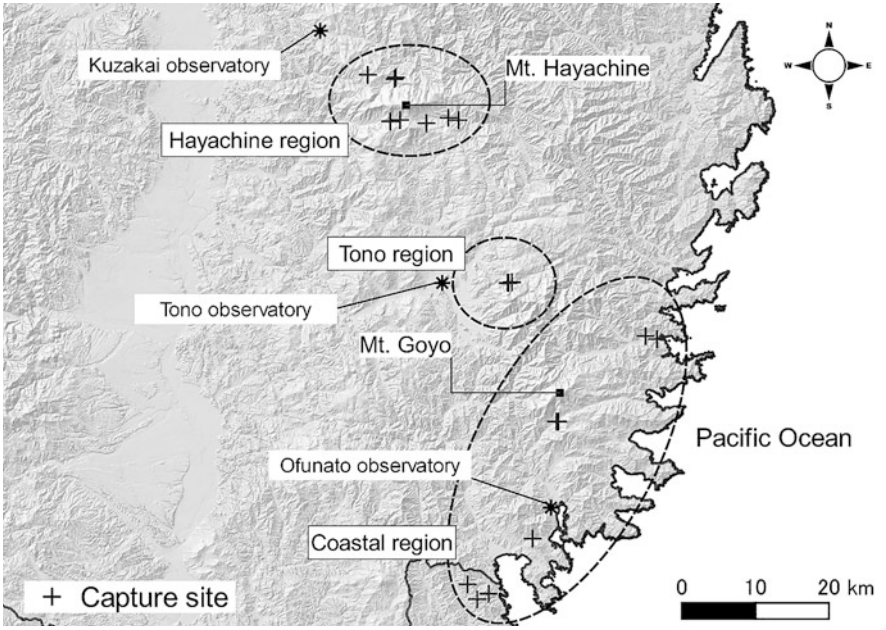

Fig. 9.2 Three regions examined in this study and locations of captured individuals. The three regions are the Hayachine region, Tono region, and Coastal region, respectively. The + indicates the location where sika deer were captured. The asterisks indicate the Kuzakai observatory in Morioka City and the Tono observatory in Tono City and the Ofunato observatory in Ofunato City, respectively

between the centroids of seasonal home ranges) was taken as the distance that the deer migrated seasonally. The path length was defined as the line connecting the beginning and end points of the seasonal migration movements. The age of captured sika deer was estimated from tooth replacement and tooth wear (Ohtaishi 1980). Using this method, the captured sika deer were classified as 1 fawn, 3 yearlings of females, and 15 adults (4 males and 11 females) (Table 9.1).

9.3 Results and Discussion

9.3.1 Migration Patterns

Of the 19 sika deer, 10 were classified as seasonal migrants and 8 as nonmigrants (Table 9.1; Figs. 9.3, 9.4, 9.5). One deer (F-3), depending on the year, was both a seasonal migrant and a nonmigrant. Three adult male deer were nonmigrants. The linear migration distance of the seasonal migrants in autumn ranged from 6.02 to 16.47 km (11.28 ± 3.28 km; mean ± SD) (Table 9.2). In studies using GPS collars in

Table 9.1 Information of sika deer fitted with GPS collars

ID	Study area	Sex	Age class	Start date	End date	Days	Migration pattern	GPS collar
H-1	Hayachine region	Female	Adult	17/9/2015	8/7/2017	660	Migratory	A
H-2	Hayachine region	Male	Adult	27/10/2015	29/5/2017	580	Nonmigratory	A
H-3	Hayachine region	Female	Adult	23/6/2016	8/2/2019	960	Migratory	A
H-4	Hayachine region	Female	Adult	9/8/2016	12/7/2019	1067	Migratory	A
H-5	Hayachine region	Female	Yearling	11/8/2016	30/3/2019	961	Migratory	A
H-6	Hayachine region	Female	Adult	22/8/2018	12/5/2020	629	Migratory	A
H-7	Hayachine region	Female	Adult	4/9/2018	12/5/2020	616	Migratory	A
H-8	Hayachine region	Female	Adult	14/8/2019	12/5/2020	272	Migratory	B
F-1	Tono region	Female	Adult	1/11/2016	19/2/2018	475	Migratory	A
F-2	Tono region	Female	Fawn	4/11/2016	14/4/2017	161	Migratory	A
F-3	Tono region	Male	Adult	19/11/2016	9/5/2019	901	Unclear	A
G-1	Coastal region	Female	Yearling	20/12/2014	26/12/2015	371	Nonmigratory	A
G-2	Coastal region	Female	Adult	13/11/2015	4/5/2018	903	Nonmigratory	A
G-3	Coastal region	Female	Adult	10/12/2015	10/3/2018	821	Nonmigratory	A
K-1	Coastal region	Male	Adult	13/10/2016	18/8/2017	309	Nonmigratory	A
K-2	Coastal region	Female	Yearling	26/10/2016	28/7/2017	275	Nonmigratory	C
K-3	Coastal region	Female	Adult	16/11/2017	19/7/2019	610	Nonmigratory	A
KA-1	Coastal region	Male	Adult	15/11/2016	31/8/2017	289	Nonmigratory	C
KA-2	Coastal region	Female	Adult	27/9/2017	12/5/2020	958	Migratory	A

ID indicates the individual number. Study regions are shown in Fig. 9.2. Start date indicates the date when the GPS collar was fitted. In individuals that completed the survey prematurely, end date indicates the date when the individual died, the collar dropped off, or the GPS collar malfunctioned. For data from individuals that were used in the survey, end date indicates the last day that data was retrieved. Sika deer that moved between summer and winter home ranges are indicated as being "migratory," while those that did not migrate are indicated as "nonmigratory." For individual F-3, the migratory pattern was treated as "unclear" as both migratory and nonmigratory years were observed. GPS collar indicates the model of GPS collar used for each individual (A: TrackM2D, LOTEK; B: Lite Track IRIDIUM420, LOTEK; C: GLT-03, Circuit design)

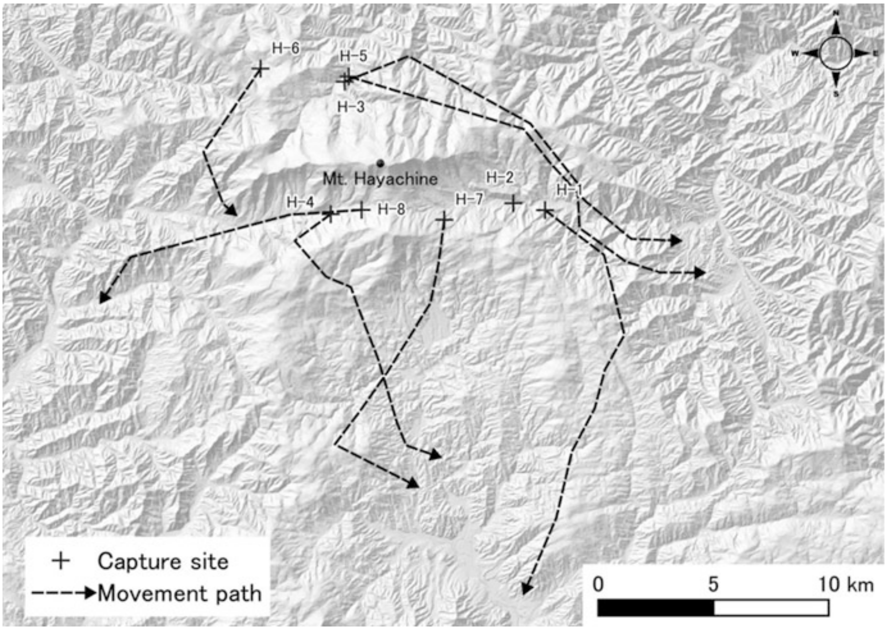

Fig. 9.3 Locations of captured individuals and direction of movement in the Hayachine region. The + indicates the location where sika deer were captured. The arrows show the migration route of each sika deer as they moved from their summer to winter home ranges

central Japan, the mean distance was 15.8 km (Takii et al. 2012a) and 9.9 km (Takii et al. 2012b), which was similar to the results reported here. The summer and winter home ranges of the individuals that were tracked over multiple years showed that sika deer generally remained in the same location (Fig. 9.6). The proportions of seasonal migrants in each region were 87.5% (seven of eight animals) in the Hayachine region, 66.7% (two of three animals) in the Tono region, and 12.5% (one of eight animals) in the coastal region.

The duration required for seasonal migration and the migration speed of each individual are shown in Table 9.2. The number of days required for the spring and autumn migration were 7.00 ± 11.40 and 7.00 ± 11.61 days, respectively (mean ± SD). The migration speed in spring and autumn was 0.35 ± 0.26 and 0.27 ± 0.16 km/h, respectively (mean ± SD). The shortest spring migration was 1 day for individuals H-5, H-7, and KA-2, and the longest spring migration was 42 days for individual H-4. The shortest autumn migration was 1 day for individuals H-5, H-6, and KA-2, and the longest autumn migration was 50 days for individual H-4. There were no similarities in the duration or speed of the migration undertaken by each sika deer. However, as in previous study (Takii et al. 2012a), the sika deer moved between their summer and winter home ranges within a relatively short period of time.

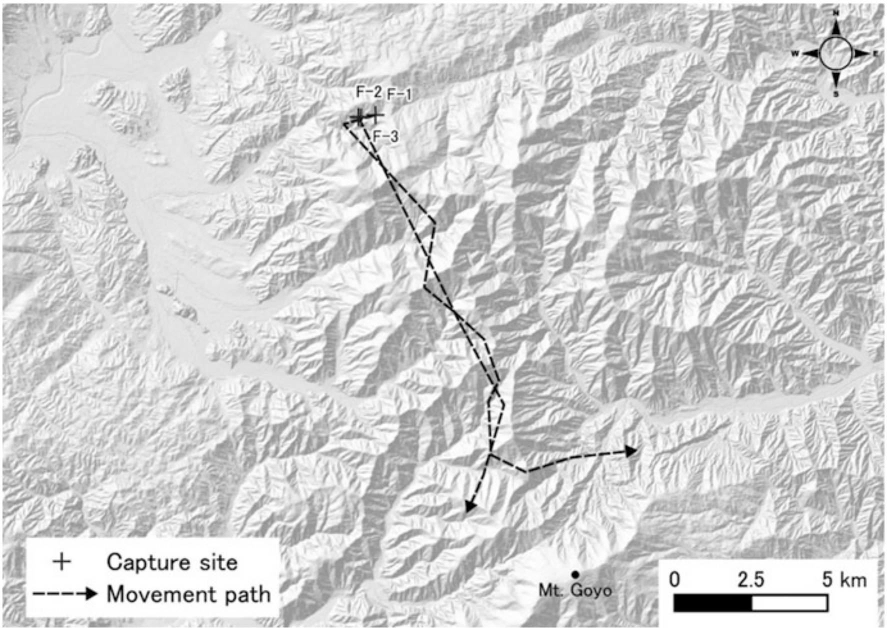

Fig. 9.4 Locations of captured individuals and the direction of movement in the Tono region. The capture site and direction of movement are indicated as in Fig. 9.3

The coastal and inland regions of the Kitakami Highlands that are inhabited by sika deer differ markedly from each other, both geographically and climatically. The coastal region is relatively warmer and experiences less snow than the inland region, while the inland region has cooler temperatures and experiences more snow. The difference in these environments is consistent with the differences observed in the migratory behavior of the sika deer described in this chapter. For example, all of the individuals in the coastal region were nonmigratory, except for individual KA-2, and all of the individuals in the inland region undertook seasonal migration, except for individual H-2, as with the result of Wildlife Management Office (2006). Therefore, using the migratory criteria employed in this study, these sika deer would also be considered nonmigrants. In the coastal population, only one individual undertook seasonal migration, so it is seemed that the sika deer population in the coastal region is essentially nonmigratory and that these individuals have not changed their behavioral patterns over time.

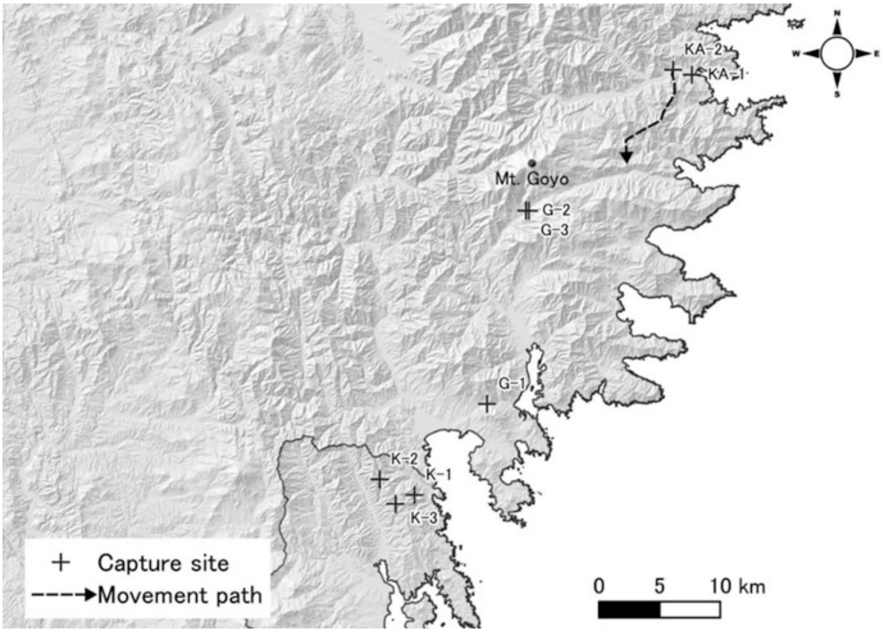

Fig. 9.5 Locations of captured individuals and direction of movement in the coastal region. The capture site and direction of movement are indicated as in Fig. 9.3

9.3.2 Timing of Seasonal Migration

In order to identify the trigger of seasonal migration, the meteorological conditions in the study area and the duration of seasonal migration in each sika deer are shown in Fig. 9.7.

As shown in Fig. 9.6, the summer and winter home ranges of the individuals that were tracked over multiple years were very similar, and the seasonal migration routes were similar. However, the timing of the start of seasonal migration in both spring and autumn was different each year. Sika deer are known to show high site fidelity, especially in summer (Uno and Kaji 2000; Igota et al. 2004), and the sika deer captured in this study also accessed the same habitat through almost the same route every year. On the other hand, the migration of large herbivores is known to be affected by factors such as food resources, weather conditions, and the risk of predation (Fryxell and Sinclair 1988). In this study, most sika deer started their autumn migration just after snowfall or when snow depth increased, although one sika deer from the coastal region started moving before snow began to fall. In addition, all individuals were observed to migrate toward the summer home range as the snow depth decreased in early spring. Takii et al. (2012b) reported that the migration of sika deer to their winter home ranges occurred before the snow depth reached 20 cm. It was also reported that snow depths of 50 cm or more limited the

Table 9.2 Duration of seasonal migration, distance migrated, and migration speed of each sika deer

ID	Sex	Age class	Spring migration				Fall migration			
			Duration (days)	Distance (km)	Path length (km)	Speed (km/h)	Duration (days)	Distance (km)	Path length (km)	Speed (km/h)
H-1	Female	Adult		7.46				13.58		
				12.97				13.00		
H-3	Female	Adult	13	16.48	21.11	0.07	11	16.47	19.72	0.08
			23	15.53	19.20	0.04	4	15.51	20.86	0.25
							14	16.36	20.43	0.06
H-4	Female	Adult	2	10.82	10.84	0.36	50	11.02	15.09	0.01
			2	11.12	11.76	0.49	4	11.21	16.86	0.19
			42	11.23	14.84	0.02	15	10.76	16.29	0.05
H-5	Female	Yearling	3	14.89	17.91	0.27	1	14.80	15.42	0.64
			1	14.70	16.59	0.69	3	14.62	16.29	0.25
							2	14.18	15.75	0.37
H-6	Female	Adult	3	6.15	10.38	0.20	1	6.36	8.90	0.49
			2	6.02	8.97	0.21	1	6.02	8.40	0.35
H-7	Female	Adult	1	9.50	9.29	1.03	2	9.33	10.16	0.38
			1	8.38	10.11	0.48	4	10.14	10.44	0.12
H-8	Female	Adult		8.04				8.05		
F-1	Female	Adult		9.48				9.44		
F-2	Female	Young					2	13.14	14.03	0.36
KA-2	Female	Adult	1	7.55	8.71	0.41	2	7.47	8.41	0.31
			2	7.78	9.10	0.34	1	7.56	8.34	0.35
			2	7.68	8.48	0.24	2	7.78	8.33	0.28
Mean (±*se*)			7.00 ±11.40	10.32 ±3.24	12.66 ±4.21	0.35 ± 0.26	7.00 ±11.61	11.28 ±3.28	13.75 ±4.37	0.27 ±0.16

ID indicates the individual number. Migration days indicate the number of days that it took to migrate between the seasonal home ranges. Distance indicates the distance, in a straight line, between the center points of the seasonal home ranges. Path length indicates the length of the line that connects the center point of the seasonal home range to each point located while migrating. Speed was calculated as the migrated distance per hour on migration days along the path length. The blanks in the columns show unclear data

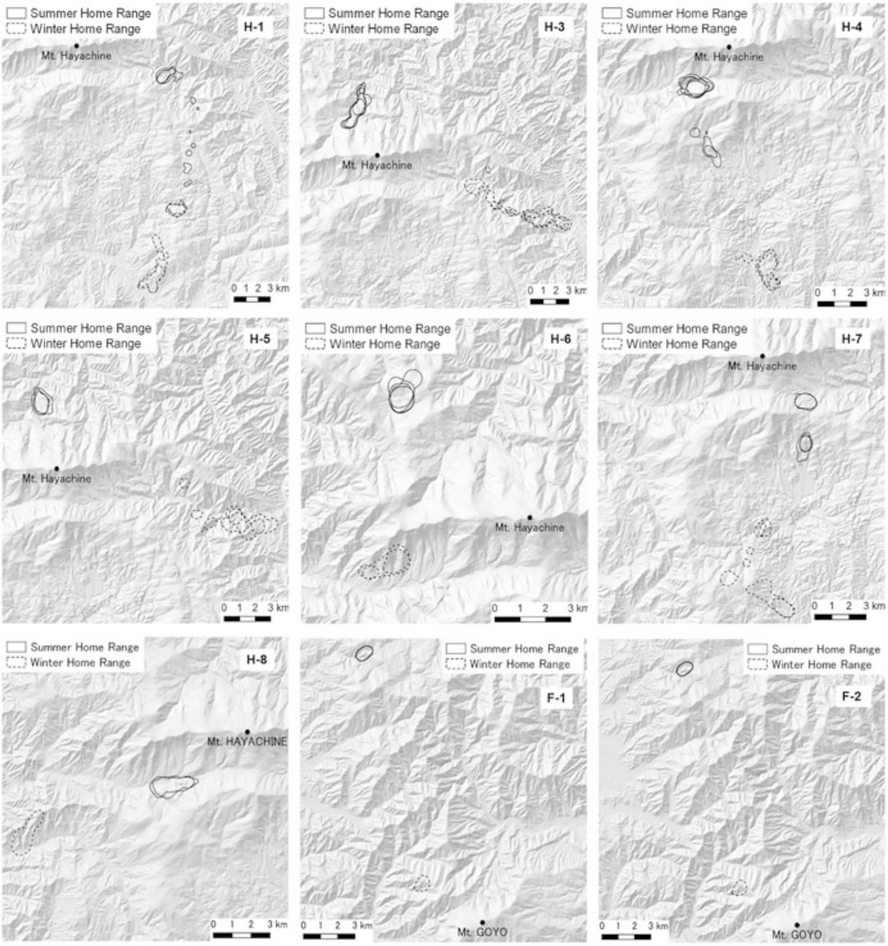

Fig. 9.6 Summer and winter home ranges of each individual. The home ranges of individuals tracked over multiple years were overlaid on the map

behavior of deer (Takatsuki 1992a, b; Morimitsu et al. 2019). In this study, it was not possible to determine the snow depth that occurred during the autumn migration because levels of snowfall in the area where sika deer were actually living were unknown. However, most of the seasonal migrants moved to lower elevation areas before the snow depth increased, suggesting that they likely responded to a snow depth of <50 cm.

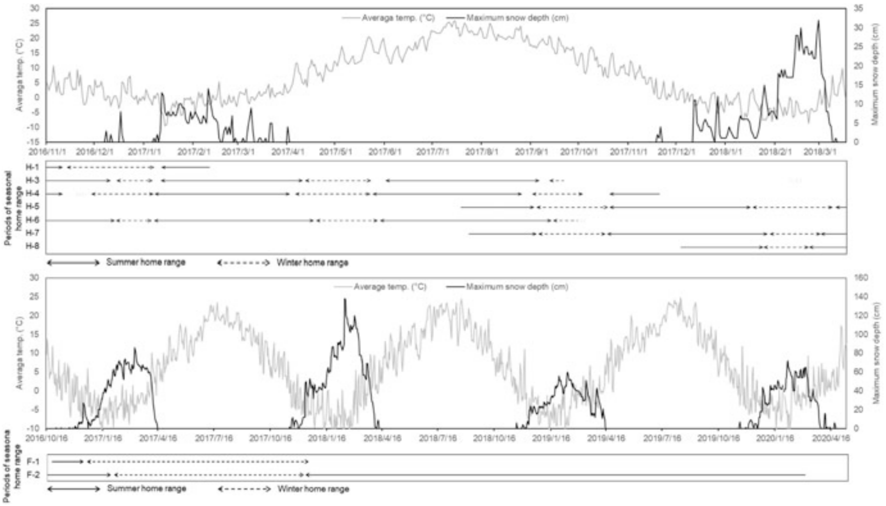

Fig. 9.7 Relationship between the average temperature (°C) in the seasonal home range and maximum snow depth (cm). For the Hayachine region, observation data were obtained from the Kuzakai observatory (39°39.0′N, 141°21.2′E, 760 m above sea level (a.s.l.)). For the Tono region, observation data were obtained from the Tono observatory (39°20.2′N, 141°32.3′E, 273 m a.s.l.). Seasonal home ranges were defined as the area in which an individual remained for more than 30 days without moving more than 2 km in any direction in 1 day (see Takii et al. 2012a)

9.3.3 Land Use Pattern in Winter Home Ranges

Table 9.3 shows the home ranges of seasonal migrants. Data showing sika deer that remained in their seasonal home range for <60 days were excluded from the analysis due to an error that would occur when analyzing the home range by the Kernel method. The summer home ranges were approximately 0.57 to 3.14 (1.44 ± 0.62) km^2, and the winter home ranges were approximately 0.59 to 4.62 (2.23 ± 1.06) km^2 (mean ± SD). In eight out of 10 sika deer, the winter home range was larger than the summer range in every year of the study period. Similarly, in Hokkaido, the winter home range was larger than the summer range, and it was considered that the distribution of higher-quality bamboo grass affected their distribution behavior (Igota et al. 2004). Since a detailed environmental analysis of the overwintering area was not conducted in this study, the status of the understory vegetation could not be determined. However, since the winter food resources of sika deer in Iwate Prefecture are limited to plants such as bamboo grass and true sedge (*Carex* spp.) (Iwate Prefecture 1990), it is likely that sika deer move about extensively in order to obtain resources efficiently for less effort. The total home range area of each individual was calculated by the fixed kernel method (150 m radius, 90%). For nonmigrants, the home range areas of females ($n = 5$) and males ($n = 3$) were 1.12 ± 0.41 km^2 and 2.03 ± 0.43 km^2, respectively, indicating that males had larger home ranges than females. However, all migrants (all females, $n = 9$) had home

Table 9.3 Home range size of each seasonal migrant

	2015		2016		2017		2018		2019	
ID	Summer	Winter	Summer	Winter	Summer	Winter	Summer	Winter	Summer	Winter
H-1	3.14	4.62	0.97	3.03	1.02					
H-3			2.46	3.10	2.01	3.96	2.09	3.22		
H-4			0.80	2.37	2.46	1.76	1.89	1.43	1.29	
H-5			1.42	2.97	1.01	3.26	1.27			
H-6							1.21	1.31	0.88	1.03
H-7							1.38	2.19	1.35	2.70
H-8									1.62	1.81
F-1			0.71	2.91	0.97					
F-2			0.57	0.59						
KA-2					1.05	1.71	1.69	1.17	1.28	0.91

ID indicates the individual number. Summer and winter in the table indicate the area of summer and winter home ranges (km^2), respectively ranges of 4.04 ± 1.72 km^2, which was larger than that of nonmigrants (Table 9.3). Home ranges were larger among males than among females in the Oku-Chichibu Mountains (Takii et al. 2012a). This may be because males are more active than females. Due to the small sample size, it was not possible to clarify the underlying reason for this behavior with certainty. Consequently, in future research, it will be necessary to increase the number of samples to verify why this occurred.

To compare the topographic characteristics of each seasonal home range, the elevation, slope, and slope direction of the GPS data of each individual were obtained, and these data were aggregated for each summer and winter home range (Table 9.4). Since similar results were obtained for almost all individuals, the analysis results for elevation, slope, and slope direction for H-3 and H-8 are shown in Fig. 9.8 as representative results. The elevation of each seasonal home range was significantly different in nine out of ten individuals (Wilcoxon rank sum test, $p < 0.001$), of which eight individuals inhabited home ranges at lower elevations in the winter compared to the summer (Table 9.4). Igota et al. (2004) conducted a telemetry study on Ezo sika deer (*Cervus nippon yesoensis*). They referred to sika deer that moved to winter home ranges that were at lower elevations compared to their summer home ranges as “downward migrants.” Conversely, they referred to deer that moved to higher-lying winter home ranges as “upward migrants.” In this study, the results of the analysis showed that most of the individuals were “downward migrants.” Using a map obtained from the Ministry of the Environment (Biodiversity Center of Japan 2020), the vegetation in the seasonal home ranges was classified into broad-leaved forests, coniferous forests, and others (cultivated land, urban area, and cutover forest), and the percentage of each vegetation type was estimated in each home range. For example, the vegetation in the summer home ranges of H-3 and H-8 comprised 13.2% and 44.0% broad-leaved forest and 85.4% and 55.4% coniferous forest, respectively. These findings showed that coniferous forest was generally more widely used than broad-leaved forest. However, the vegetation in the winter home ranges of H-3 and H-8 comprised 68.2% and 51.2% broad-leaved forest and 29.4% and 37.7% coniferous forest, respectively. Thus, in winter, the broad-leaved forest was more widely used. These results need to be verified in greater detail by examining the understory vegetation in the future.

The upward migrants of Ezo sika deer used mainly coniferous forests (Igota et al. 2004). Based on an analysis of aerial photographs, KA-2, which was the one of the upward migrants investigated in this study, also seemed to use areas of coniferous cover. KA-2 was captured close to the town of Kamaishi City where it primarily used riverine areas. In autumn, this individual fed upon the grass growing in cutover areas near high-voltage lines and in abandoned agricultural fields. Given that this individual appeared to prefer areas near human settlements, it was difficult to determine whether the behavior exhibited by this individual is typical of sika deer; consequently, it may be better to treat it as an exception in this study.

In the slope direction analysis, significant differences were observed between summer and winter home ranges in all ten individuals (Watson-Wheeler test, $p < 0.001$); in nine of these sika deer, the mean slope direction in the winter home range was more southerly than that in the summer home range (Table 9.4). There

Table 9.4 Relationship between the elevation, slope direction, and slope in summer and winter home range

	ID	Wilcox test	Summer	Winter
Elevation	H-1	$p < 0.001$	648.7 ± 77.4	598.9 ± 148.1
	H-3	$p < 0.001$	734.6 ± 97.4	555.9 ± 112.3
	H-4	$p < 0.001$	984.5 ± 82.3	448.3 ± 50.5
	H-5	$p < 0.001$	672.8 ± 57.2	465.7 ± 101.5
	H-6	$p < 0.001$	901.3 ± 42.6	855.1 ± 97.2
	H-7	$p < 0.001$	994.1 ± 93.6	583.7 ± 173.1
	H-8	$p < 0.001$	792.0 ± 81.1	465.1 ± 158.8
	F-1	$p = 0.807$	715.6 ± 56.7	664.9 ± 173.1
	F-2	$p < 0.001$	719.3 ± 18.3	817.4 ± 75.4
	KA-2	$p < 0.001$	84.9 ± 79.3	278.9 ± 94.5
	ID	Watson-wheeler test	Summer	Winter
Slope direction	H-1	$p < 0.001$	17.8 ± 1.4	−127.4 ± 1.7
	H-3	$p < 0.001$	−8.8 ± 1.0	111.2 ± 1.2
	H-4	$p < 0.001$	−35.6 ± 0.9	156.2 ± 1.6
	H-5	$p < 0.001$	−28.0 ± 1.2	73.9 ± 1.6
	H-6	$p < 0.001$	−85.3 ± 1.4	179.9 ± 0.6
	H-7	$p < 0.001$	70.3 ± 1.3	94.7 ± 1.8
	H-8	$p < 0.001$	−32.8 ± 0.8	161.6 ± 1.0
	F-1	$p < 0.001$	−165.4 ± 0.9	−34.7 ± 2.3
	F-2	$p < 0.001$	−41.9 ± 1.3	−170.1 ± 0.8
	KA-2	$p < 0.001$	−19.4 ± 1.6	130.4 ± 0.8
	ID	Watson-wheeler test	Summer	Winter
Slope	H-1	$\mathrm{p} = 0.0027$	18.2 ± 0.1	18.0 ± 0.1
	H-3	$p < 0.001$	21.0 ± 0.1	25.0 ± 0.2
	H-4	$p < 0.001$	21.5 ± 0.1	21.1 ± 0.2
	H-5	$p < 0.001$	21.3 ± 0.1	28.4 ± 0.1
	H-6	$p < 0.001$	13.7 ± 0.1	27.6 ± 0.1
	H-7	$p < 0.001$	22.6 ± 0.1	20.1 ± 0.1
	H-8	$p < 0.001$	20.0 ± 0.1	25.2 ± 0.2
	F-1	$p < 0.001$	29.8 ± 0.2	33.6 ± 0.1
	F-2	$p < 0.001$	23.0 ± 0.2	32.3 ± 0.1
	KA-2	$p < 0.001$	19.2 ± 0.3	25.0 ± 0.2

ID indicates the individual number. Summer and winter indicate the aggregate value of the summer and winter home range, respectively. Each value is shown as mean ± standard deviation. P-values represent the results of the Wilcox and Watson-Wheeler tests

was also a significant difference in slope between the summer and winter home ranges in nine out of ten individuals (Watson-Wheeler test, $p < 0.001$); in eight of these sika deer, the mean slope of the winter home range was steeper than that of the summer home range (Table 9.4). Thus, in winter, most sika deer used sunny southern slopes in low-elevation areas with little snow cover and steep slopes in terrain where it is difficult for snow to accumulate.

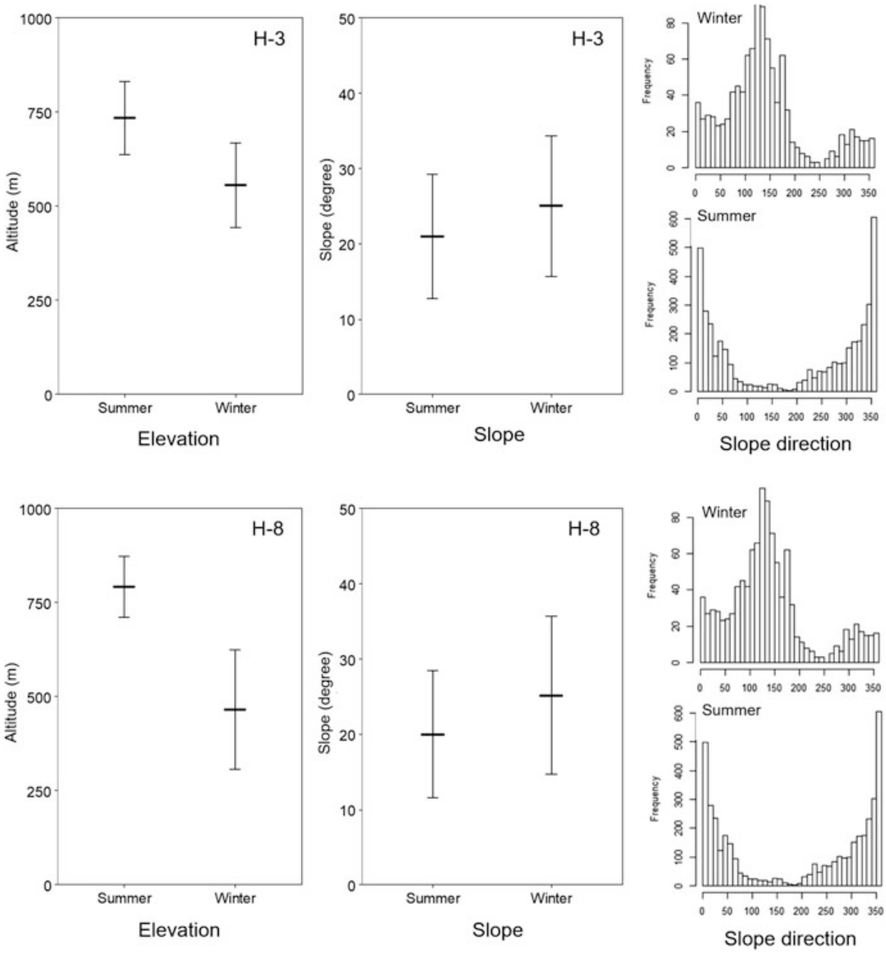

Fig. 9.8 Representative analytical results for movements of individuals H-3 and H-8 considering elevation, slope, and slope direction. The center line and error bar for elevation and slope show the mean value and standard deviation, respectively. Winter (top figure) and summer (bottom figure) in the bar graph showing slope direction indicate the results of the winter and summer home ranges, respectively. The x-axis shows the slope direction: due north is 0° and 360°, and due south is 180°. Y-axis (frequency) shows the number of GPS data points

Since 2000, the distribution of sika deer has expanded rapidly toward the inland regions of the Kitakami Highlands. Compared to other regions discussed in this chapter, the higher-lying Hayachine region experiences heavier snowfalls and lower temperatures in winter. It was therefore initially unclear whether sika deer were overwintering in this region. The primary objective of the GPS telemetry surveys in Hayachine region was to determine where sika deer overwinter. Except for one male (H-2), individuals captured on the southern side of Mt. Hayachine moved southward, and individuals captured on the northern side moved to the east and to the south where there was less snow. These behavioral patterns were typical of downward migrants. The Tono region is also characterized by having low temperatures and heavy snowfalls in winter. Like the Hayachine region, the sika deer in this region likely also experienced difficulty in obtaining food in the winter. One of the individuals captured in the Tono area moved repeatedly between the summer and winter home ranges but was essentially a downward migrant. By expanding their habitat to include areas that experience severe climate, sika deer in inland regions start migrating when the snow falls, as they do in Hokkaido (Igota et al. 2004) and Nagano Prefecture (Takii et al. 2012a, 2012b; Izumiyama et al. 2009). For autumn migration, sika deer are considered to move to lower lying areas with south-facing slopes where the temperature is higher and snow cover is relatively sparse, where they feed on grass. Bamboo grass has been reported to be an important and high-quality winter food resource in Hokkaido (Igota et al. 2004). Although the understory vegetation was not analyzed in this study, it is highly likely that the distribution of bamboo grass overlapped with the overwintering areas, as bamboo grass is also an important food resource for deer in winter in Iwate Prefecture (Takatsuki 1986). In addition, there are numerous farms and grasslands in the mountains of the Kitakami Highlands, and these environments may be used as stopover points during seasonal migration or as overwintering areas themselves. In particular, in the Tono region, there are numerous pastures at altitudes of between 800 and 1300 meters a.s.l. In the Kitakami Highlands, there are many pastures that are currently unmanaged due to the release of radioactive cesium into the atmosphere after the nuclear power plant accident. The possibility that these grasslands are also important overwintering areas is high, and detailed field surveys based on GPS location information should be undertaken in the future.

9.4 Future Investigations

Sika deer in the Tohoku region have continuously inhabited part of coastal areas after widespread extirpation elsewhere. The reasons for this are considered to be because of the lower snowfall and relatively warm climate near the coast, which together have enabled sika deer to maintain high population densities. The range of behavioral activities in these populations was relatively small, and the sika deer in these regions were essentially nonmigratory. However, in response to a decrease in both hunting pressure in areas further inland, and a decrease in human activities in mountainous areas due to the declining human birthrate and aging population, these sika deer populations subsequently expanded their distribution to inland areas. Consequently, sika deer became seasonal migrants in response to environmental conditions such as lower temperatures and high snowfall in inland areas in winter. This dispersal toward inland areas, which includes higher-altitude areas such as Mt. Hayachine, occurred relatively suddenly in the last 20 years. This phenomenon shows that sika deer are highly adaptable and can survive in severe environments in a short period. However, despite the severe environmental conditions around

Mt. Hayachine, one individual (H-2) remained in the area over winter. It is considered that this individual might have overwintered in areas of coniferous cover that had high-quality bamboo grass, as has been reported in Hokkaido (Igota et al. 2004). Similar environmental analyses using detailed field surveys and continuous telemetry surveys are therefore considered necessary in the Tohoku region.

In response to a certification system for professional culling that was introduced after an amendment to the Wildlife Protection and Proper Hunting Law in 2014, the hunting pressure on sika deer populations has increased rapidly in the Tohoku region. In particular, the number of sika deer culled has increased markedly in the area surrounding Mt. Goyo, primarily due to the high population density of sika deer in the area and the high culling efficiency of the hunters. It is therefore necessary to examine how sika deer behavior will be affected by the increase in hunting and nuisance control culling in the future (e.g., Kamei et al. 2010).

The individual KA-2, which was captured in the town of Kamaishi City, was the only migrant in the coastal region. Numerous buildings were destroyed in the city by the tsunami that followed the Great East Japan Earthquake. Moreover, large expanses of forests were felled in order to develop residential land and relocate residents to higher-lying ground, and it seems that this artificial habitat disturbance has affected the behavior of sika deer in this region. Sika deer have been hunted in the daytime in close proximity to buildings, along roads, and in parts of the town that had become overgrown; these are behavioral patterns that were not observed before the earthquake disaster. It is also possible that migration from the town was triggered by hunting activities. It is considered necessary to investigate how the behavior of sika deer in the coastal regions was affected by the earthquake disaster, with a particular focus on the effects of human activities. In addition, mega-solar power plants have been constructed in the coastal region after the earthquake disaster, and some individuals have successfully utilized these sites and the maintenance roads for power-transmission lines as habitat. It is considered that nonmigrants in the coastal region have successfully adapted to areas that have been developed after the earthquake disaster.

The Specific Wildlife Management Planning System for each prefecture in the Tohoku region aims to eradicate sika deer in areas where they have newly settled. Before the Meiji era, sika deer had been widely distributed in the Tohoku region and coexisted with humans, and some people are cautious about eradication. However, considering the enormous damage caused by deer to agriculture and forestry in recent years, reducing their population densities is considered to be necessary. There are numerous rare and endemic plant species in the alpine zone of Mt. Hayachine, and the increase in feeding damage, e.g., bite marks on plant leaves by sika deer, has been considerable in recent years. Therefore, an accurate understanding of seasonal migration during the hunting season in winter is very important for reducing sika deer densities in some areas, and it is crucial to identify overwintering areas by continuous telemetry surveys.

Recently, sika deer have been observed on the western side of the Ou Mountains. This area, which faces the Sea of Japan, is one of the heaviest snowfall areas in Japan and has a steep topography. Since it is clearly a different environment from the

Kitakami Highlands, the behavioral patterns of the sika deer in the region may be quite different from those of the sika deer described in this chapter. In order to develop appropriate conservation and management strategies for sika deer in the Tohoku region, it may be necessary to conduct telemetry surveys in these new areas.

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Chapter 10
Movement Patterns of Sika Deer in the Mountainous Regions of Central Honshu

Akiko Takii and Shigeyuki Izumiyama

Abstract We conducted GPS (VHF) telemetry in (1) the Okuchichibu Mountains, a less snowy mountainous region; (2) the Kirigamine Highland, Honshu's most extensive grassland with relatively heavy snowfall; and (3) the Southern Japan Alps, an alpine mountainous region that holds the greatest altitudinal difference in Honshu. Thirty-two deer were migrants, 10 were residents, and 4 were dispersers. The mean migration distances were 9.9–15.8 km. We compared the home range characteristics between the three study areas and discussed the driving factors of migration. The Okuchichibu Mountains was the only area where the mean altitudes did not differ between seasons. Considering the low hunting pressure and the road density in the winter, deer in the Okuchichibu Mountains migrated to avoid anthropogenic effects during the winter. In the Kirigamine Highland and the Southern Japan Alps, deer migrated from a high-altitude area to a lower-altitude area and were considered to migrate to avoid deep snow during the winter. In the Kirigamine Highland, deer stayed in the grasslands until snowfall had covered the vegetation. Seven migrants in the Southern Japan Alps inhabited the alpine zone during the summer and exhibited dramatic altitudinal migration. These deer stayed in the alpine zone from the early to the end of the plant's growing period, to access highly nutritious plants in the alpine zone.

10.1 Introduction

In medium- to high-altitude regions, cervids usually demonstrate seasonal migration due to snowfall that limits the abundance of forage (e.g. D'Eon and Serrouya 2005; Brinkman et al. 2005; Cagnacci et al. 2011; Igota et al. 2004). Conversely, cervids that inhabit mountainous regions are known to demonstrate altitudinal migration. They migrate from high-elevation summer home range to lower-elevation winter range (Nicholson et al. 1997; Takatsuki et al. 2000; Ramanzin et al. 2007; Mysterud

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A. Takii (✉) · S. Izumiyama
Shinshu University Institute for Mountain Science, Nagano, Japan
e-mail: akikomt@shinshu-u.ac.jp; izumiys@shinshu-u.ac.jp

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et al. 2011). Moreover, they seldom demonstrate reverse altitudinal migration (Loft et al. 1984; Igota et al. 2004; Pépin et al. 2008).

For deer inhabiting high latitudes with severe winter climates, their body fat reserves are crucial for winter survival, and body fat accumulation largely depends on food intake during summer and fall (Mautz 1978). Both females and males must gain body mass from highly nutritious forage during summer. These resources are essential for females for lactation and sufficient conditions during pregnancy (Cook et al. 2004). In contrast, males need these resources to prepare for the breeding season in autumn (Barboza et al. 2004). Fryxell (1991) introduced the forage maturation hypothesis, which states that the common driver of altitudinal migration is the benefit of high forage quality at high elevations. Several studies on montane ungulates document that migratory deer had greater access to higher-quality forage (Hebblewhite et al. 2008; Bischof et al. 2012; Debeffe et al. 2017). The increasing nitrogen content in plants at increasing altitudes is general (Körner 1989). Albon and Langvatn (1992) revealed that plants had high crude protein at high elevations during the early growing season. Other factors of seasonal migration include predator avoidance (Fryxell and Sinclair 1988; Hebblewhite and Merrill 2009), hunting pressure (Kamei et al. 2010), and human activity (Dingle and Drake 2007). However, the factors that contribute to the seasonal migration of sika deer inhabiting the mountainous regions of Honshu have not been determined.

This chapter describes the seasonal movements of sika deer (*Cervus nippon*) in three regions of Nagano Prefecture, Honshu (Fig. 10.1). We conducted GPS (VHF) telemetry in (1) the Okuchichibu Mountains, a less snowy mountainous region; (2) the Kirigamine Highland, Honshu's most extensive grassland with relatively heavy snowfall; and (3) the Southern Japan Alps, an alpine mountainous region that holds the greatest altitudinal difference in Honshu. First, we describe the movement patterns of deer in these areas and compared the ratio of migrants and home ranges, and second, we compare the topographical (altitude, aspect, and slope) factors, coniferous cover, and anthropogenic factors (road density) of the seasonal home ranges of migratory deer and discuss the factors associating with migration. In addition, we describe the dispersals that we observed in the Kirigamine Highland.

10.2 Study Area

10.2.1 Okuchichibu Mountains

We captured deer in the Kawakami Village, Nagano Prefecture, located at the foothills of the western Okuchichibu Mountains. The Okuchichibu Mountains extend across the Nagano, Yamanashi, Saitama, and Gunma prefectures. The topography of the mountainous area includes steep slopes with deep valleys and rocky mountain ridges. Two-thirds of the study area is part of Chichibu-Tama-Kai National Park, established in 1950. A large wildlife protection area (344.7 km^2) was established mainly in high-altitude areas.

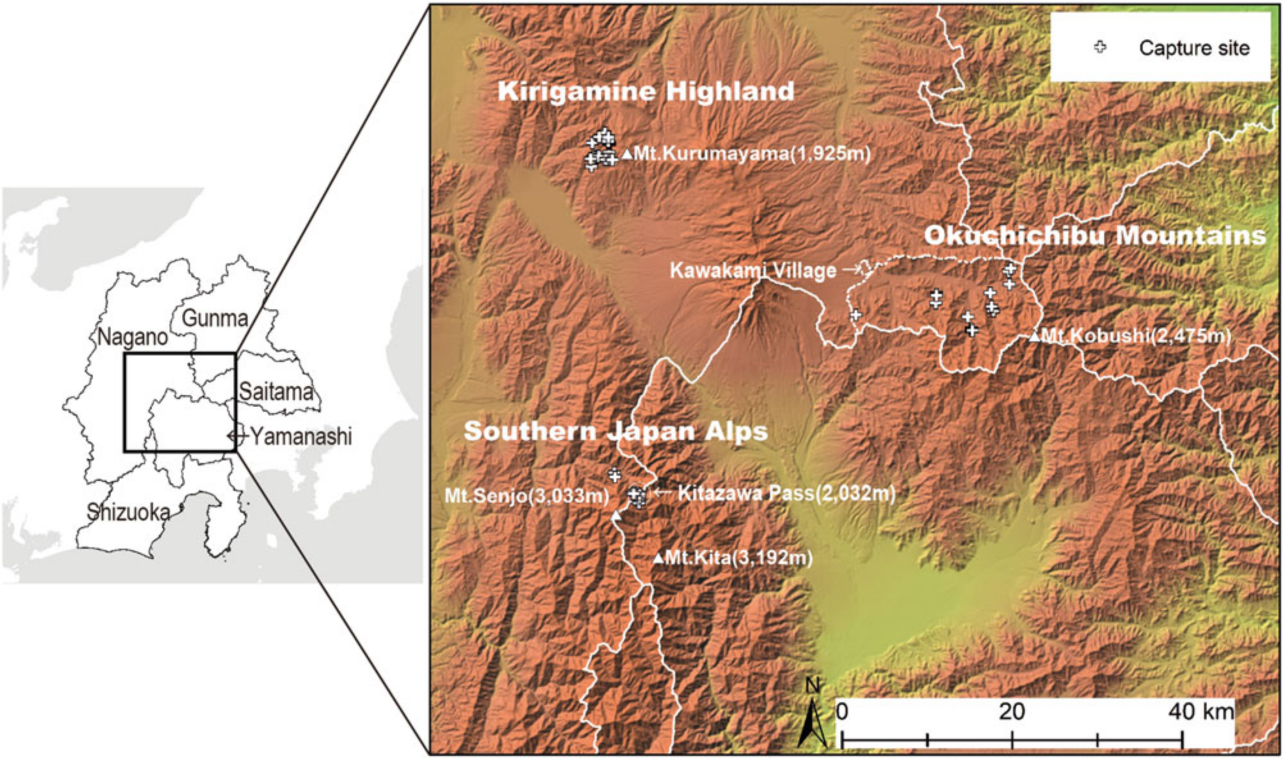

Fig. 10.1 The capture site of deer in three study areas. Major mountain peaks in each study area are shown on the map

Elevation. We captured deer at 1380 to 1510 m a.s.l. The elevation in this study area ranges from 530 to 2601 m, and there are >20 peaks with ≥2000 m a.s.l.

Vegetation. In the subalpine zone (1700–2500 m a.s.l.), evergreen coniferous forests dominate. The landscape of the Kawakami Village upper montane zone (1000–1700 m a.s.l.) significantly differs from the rest of the study area. *Larix kaempferi* (Japanese larch) plantations and croplands (e.g., lettuce) distribute widely in the Kawakami Village. However, deciduous broad-leaved forests consisting mainly of *Fagus crenata* and *Quercus crispula* (Japanese oak) predominate in other areas. In the lower montane zone (< 1000 m a.s.l.), patches of *Cryptomeria japonica* (Japanese cedar) and *Chamaecyparis obtusa* (Japanese cypress) plantations can be found, as well as deciduous broad-leaved forests.

Climate. In 2000–2009 at the Nobeyama Meteorological Station (35°57' N, 138°28'E; 1350 m a.s.l.), the annual mean temperature was 7.2°C, and the annual mean precipitation, including snow, was 1435 mm (Meteorological Data of Nagano Prefecture, Nagano Local Meteorological Observatory, Nagano). According to the 30-year means for 1971–2000, the study area's maximum snow depth, including the highest ridges, ranged from 9 to 44 cm (Japan Meteorological Agency 2002).

Deer density. The estimated densities of sika deer at two areas of Kawakami Village areas in 2004 and 2010 were 6.7–8.2 and 4.5–15.3 deer/km^2, respectively (Nagano Prefecture 2011).

Deer hunting. In Kawakami Village, the number of deer harvested through controlled kill and game hunting dramatically increased from 2007 to 2009 (152 deer, 287 deer, and 852 deer harvested in 2007, 2008, and 2009, respectively). Deer hunting is allowed in the hunting zones from 15 November to 15 February.

10.2.2 Kirigamine Highland

We captured deer that stayed in the Kirigamine Highland during the summer and monitored their seasonal movements in the surrounding area. Kirigamine Highland extends in and along the west of Mt. Kurumayama (36°06'N, 138°11'E; 1925 m a.s.l.). Although the topography above ca. 1600 m is rolling, it is relatively steep with narrow valleys in low elevations.

Elevation. We captured deer at 1400 to 1640 m a.s.l. at Kirigamine Highland. The study area includes the Yatsugatake Mountains, which is located east of the Kirigamine Highland. The elevation in this study area ranges from 760 to 2899 m, and there are 15 peaks with ≥2000 m a.s.l.

Vegetation. The Kirigamine Highland is characterized by large sections of secondary grasslands, dominated by *Calamagrostis longiseta* and *Miscanthus sinensis* (Nishimura et al. 1997). The grasslands cover >80% of the vegetation above 1700 m a.s.l. (Ozeki et al. 2006). Deciduous broad-leaved forests, evergreen coniferous forests, and Japanese larch plantations also distribute (Suzuki and Yano 1981). Most of the area between 1100 and 2000 m a.s.l. is covered by Japanese larch plantations, whereas the area below 1100 m a.s.l. is surrounded by cultivated lands and small villages.

Climate. In 1985−2007 at Washigamine Hütte (1660 m a.s.l.), located to the west of Yashimagahara Marsh, the mean annual temperature was 5.9°C, mean annual precipitation excluding snow was 1328 mm, and mean maximum snow depth was 75.2 cm (Hosoda and Taguchi 2009).

Deer density. Although sika deer were not common to the Kirigamine Highland until the early 1990s, the number of deer increased from 2004 to 2009 (Kishimoto et al. 2010). The estimated densities of sika deer at three adjacent areas of the Kirigamine Highland in 2004 and 2010 were 1.0−4.9 and 5.7−63.9 deer/km^2, respectively (Nagano Prefecture 2011). Contrarily, sika deer have been common in the surrounding areas of Kirigamine (Suwa Educational Association 1981), and the estimated density of sika deer at the southern part of the Yatsugatake Mountains was 23.0 deer/km^2 in 2004 and 26.9 deer/km^2 in 2010 (Nagano Prefecture 2011).

Deer hunting. Most of the Kirigamine Highland (ca. >1600 m a.s.l.) is designated as a wildlife protection area, where hunting is generally prohibited.

10.2.3 Southern Japan Alps

We captured deer in the northern part of Southern Japan Alps and monitored their seasonal movements in the surrounding area. The elevation in the study area exhibits the greatest altitudinal gradient in Honshu. Contrary to the rolling terrain at the ridgeline and the valley floor, most of the area is characterized by complex terrain with steep slopes and deep valleys. The study area was designated as South Alps National Park by the Ministry of the Environment in 1964. Most of the sites above 2000 m a.s.l. are either designated "special protection zones" or "special zones" consisting of highly vulnerable vegetation. Above 2030 m a.s.l., no roads exist, and the forest roads are closed, except for permitted vehicles during the summer.

Elevation. We captured deer at 1660 to 2036 m a.s.l. The elevation in this study area ranges from 400 to 3193 m, and there are four peaks with ≥3000 m a.s.l., including Mt. Kita (35°40'N, 138°14'E; 3193 m a.s.l.; the second tallest mountain in Japan) and Mt. Senjo (3033 m a.s.l.).

Vegetation. Vegetation distinctively changes with elevation. Ridgelines >2700 m a.s.l. are the forest limit, where *Pinus pumila* (Japanese stone pine) and alpine meadow (including snowbed grassland, windblown meadow, and windblown heath) dominate. *Betula* (*Betula ermanii*) forests distribute mainly in the subalpine to alpine zones (2000–2700 m a.s.l.). Tall grasslands also distribute in this area. Evergreen natural coniferous forests (mainly composed of *Tsuga diversifolia*, *Abies veitchii*, and *A. mariesii*) distribute widely in subalpine and alpine zones (1800–2700 m a.s.l.; Iijima and Nagaike 2015). Deciduous broad-leaved forests (mainly composed of beech and Japanese oak) and Japanese larch plantations distribute mostly in the upper montane zone (1000–1800 m a.s.l.). In the lower montane zone (<1000 m a.s.l.), evergreen coniferous plantations, *P. densiflora*

(Japanese red pine) forests, and deciduous broad-leaved forests are distributed in patches (Ministry of the Environment 1997).

Climate. The climate is characterized by high precipitation in the summer and relatively low precipitation in the winter. At 2900 m a.s.l., the mean daily temperature, minimum temperature, and maximum temperature were estimated to be 0.6°C, –15.3°C, and 21.3°C, respectively (Ishida et al. 2014).

Deer density. Before 1984, sika deer had never been observed in the alpine area (Shigeyuki Izumiyama unpublished data). The initial observation of sika deer in alpine zones was in the early 1990s, and herbivory on alpine plants became apparent in the early 2000s (Motojima 2009; Nagaike 2012). The estimated deer density at the foothills of the Southern Japan Alps rapidly increased from 2004 (22.7 deer/km^2) to 2010 (47.6 deer/km^2) (Nagano Prefecture 2011).

Deer hunting. Most of the area above ca. 2000 m a.s.l. is a wildlife protection area, where hunting is prohibited. However, controlled kill of sika deer has been conducted in the subalpine zone of the forest road since 2010.

10.3 Methods

10.3.1 Deer Capture and Tracking

We captured deer using a dart gun with a ketamine-xylazine mixture as a tranquilizer. Deer age was estimated from tooth replacement, as fawn, yearling, and adults. We received an academic capture permit from the Nagano and Yamanashi prefectures to capture the deer.

We captured 13 deer (7 females and 6 males, including 3 yearlings) in the western part of Okuchichibu Mountains (Kawakami Village; 2009), 32 deer (22 females and 10 males, including 1 female fawn and 4 male fawns) in the Kirigamine Highland (2008–2011), and 12 deer (3 females and 9 males) in the northern part of Southern Japan Alps (around Kitazawa Pass, 2007–2010). We attached GPS collars (Tellus5H1D, Followit AB, Lindesberg, Sweden; GPS PLUS-1, VECTRONIC Aerospace GmbH, Berlin, Germany) to a total of 37 deer in 3 study areas and attached VHF collars (Advanced Telemetry Systems, Isanti, Minnesota, USA) to 20 deer in the Kirigamine Highland.

The GPS collars were programmed with 15-min to 3-h relocation schedules. For VHF-collared deer, we triangulated deer locations every 3−10 days using a handheld three-element Yagi antenna and portable receiver (Yaesu FT817, Yaesu Musen, Tokyo, Japan) from May 2008 to July 2010. We located most of the VHF-collared deer during the day using more than three telemetry bearings. The mean location error from the known location was 97 ± 60 m ($n = 13$).

10.3.2 Data Analysis

Movement pattern. We analyzed the movement patterns of deer with a tracking period of more than 6 months. We delineated summer and winter home ranges for each deer that deer stayed in a specific area for more than 25 days without moving further than 2 km to any direction within a day. We defined the deer as “migrant” if the summer and winter home range did not overlap. Conversely, we defined the deer as “resident” if the deer had overlapping summer and winter home ranges. Moreover, we defined the deer as “dispersers” if the fawns moved from their natal home range and formed a nonoverlapping home range.

Migratory movement. We defined autumn migration as a movement from the summer to the winter home range and spring migration as a movement from the winter to the summer home range. We recorded the arrival and departure date of each seasonal home range. To estimate the approximate date of departure and arrival of VHF-collared deer, we calculated the median date of the first and the last day observed in seasonal home ranges.

We calculated the center of activity (COA) by averaging the longitude and latitude of the GPS and VHF collar’s relocation fixes at each seasonal home range (Hayne 1949). We calculated the migration distances using the straight-line distance (linear distance) between the COA of the summer and winter home range. We calculated the migration distance between the summer and the initial winter home range for the deer wintered in multiple areas. We used the home range with a longer duration of stay for analysis. We used the Kruskal-Wallis test to compare the migration distance between three study areas.

Home range. We calculated the 95% fixed-kernel (FKD: Worton 1989) summer and winter home ranges using the “adehabitat” package for the R software (Calenge 2006) with reference smoothing ad hoc (Pellerin et al. 2008). For residents, we defined April to November as “summer” and December to March as “winter.” For GPS-collared deer, we used GPS fix with more than 1-hr interval to calculate home range. For VHF-collared deer, seasonal home ranges were calculated if the deer were located 30 times in a season. We used the Mann-Whitney *U* test to compare the seasonal home range between study areas. Where the deer were tracked for more than 2 years, we evaluated the fidelities to the seasonal home ranges and calculated the distances between the COA in successive summer/winter home ranges. We compared the distances between the COA in successive years between summer and winter by Mann-Whitney *U* test.

Seasonal home range use. We compared the summer and the winter home ranges in terms of the used elevation, slope, aspect, coniferous cover, and road density. We used a 10-m digital elevation model (Fundamental Geospatial Data: National Land Agency, Geospatial Information Authority of Japan, Tokyo) to generate the elevation, slope, and aspect of each GPS fixes (more than 1-hr intervals) using the ArcGIS software. Since 18 out of 27 deer used VHF telemetry in the Kirigamine Highland, for both VHF- and GPS-collared deer, elevation was calculated using the COA of summer and winter home range. We used only GPS-collared deer data to analyze other variables in the Kirigamine Highland. We calculated the percentage of steep slope (≥30°), southerly aspects (135° to 225°), and coniferous cover (evergreen natural coniferous forests and evergreen coniferous plantations) of the GPS fixes in the seasonal home range. We used the vegetation map of sixth and seventh national surveys on the natural environment to reclassify vegetation (Biodiversity Center of Japan 2004). To evaluate the level of human disturbance in the seasonal home ranges, we calculated the paved and dirt road densities (m/ha) for each seasonal 95% home range. Roads closed during the winter were excluded from the winter home range. We used Wilcoxon signed-rank test to compare the elevation, southerly aspect ratio, steep slope ratio, coniferous cover ratio, and road density between summer and winter home range at each study area. We compared each variable between the three study areas using Kruskal-Wallis tests.

Dispersals. We analyzed the dispersals in the Kirigamine Highland, the only study area where we captured fawns. To estimate the approximate date of departure at the natal home range, we calculated the median date of the last day observed in the pre-dispersal home range and the first day observed in the postdispersal home range. We evaluated the seasonal movement pattern of dispersed deer that acquired ≥8 months of tracking at the postdispersal home range.

All data were expressed as mean ± standard deviation.

10.4 Results

10.4.1 Comparison of Movement Characteristics Among Three Regions

10.4.1.1 Movement Pattern

We used 6 deer (5 females and 1 male, including 2 female yearlings) in Okuchichibu Mountains, 27 deer (20 females and 7 males, including 1 female fawn, 2 female yearlings, 4 male fawns, and 1 male yearling) in the Kirigamine Highland, and 10 deer (2 females and 8 males) in the Southern Japan Alps to analyze the movement pattern (Table 10.1).

All the deer were migrants in the Okuchichibu Mountains (Fig. 10.2), whereas the deer were either migrants or residents in the Kirigamine Highland and the Southern Japan Alps (Table 10.2). In the Kirigamine Highland, a total of four male fawns dispersed from their natal home range, and we were able to track the postdispersal movement of three males (1 male was killed during dispersal). Seventeen deer (14 females and 3 males, 65%) were migrants and 9 deer (6 females and 3 males, 35%) were residents in the Kirigamine Highland (Fig. 10.3). Of the ten deer analyzed in the Southern Japan Alps, nine deer (two females and seven males) were migrants and one male deer was resident (Figs. 10.4 and 10.5).

Table 10.1 List of analyzed sika deer captured in the Okuchichibu Mountains (OM), Kirigamine Highland (KH), and the Southern Japan Alps (SA) during 2007–2011

Deer ID	Sex	Age	Body mass (kg)	Movement strategy	Date of capture	Collar type	Tracking period (months)	Number of fixes
OM1	F	Adult	51	Migrant	15 April 2009	GPS	11	14,260
OM2	F	Yearling	46	Migrant	22 April 2009	GPS	11	15,499
OM6	F	Yearling	38	Migrant	24 April 2009	GPS	11	8628
OM7	F	Adult	48	Migrant	14 May 2009	GPS	11	7462
OM12	M	Adult	92	Migrant	20 May 2009	GPS	7	8087
OM13	F	Adult	46	Migrant	21 May 2009	GPS	10	13,152
KH1	M	Yearling	36	Migrant	23 April 2008	VHF	26	90
KH2	M	Fawn	36	Dispersal/resident	23 April 2008	VHF	26	87
KH3	F	Adult	56	Migrant	23 April 2008	VHF	26	93
KH4	F	Fawn	28	Resident	29 April 2008	VHF	14	58
KH5	F	Adult	66	Migrant	30 April 2008	VHF	26	99
KH6	F	Adult	56	Migrant	30 April 2008	VHF	26	85
KH7	M	Fawn	26	Dispersal/resident	1 May 2008	VHF	26	102
KH8	F	Adult	47	Resident	1 May 2008	VHF	26	98
KH9	M	Adult	57	Resident	7 May 2008	VHF	18	77
KH10	F	Yearling	42	Migrant	8 May 2008	VHF	26	106
KH11	F	Adult	72	Resident	9 May 2008	VHF	9	50
KH12	F	Adult	50	Migrant	21 May 2008	VHF	25	93
KH13	M	Fawn	35	Dispersal	22 May 2008	VHF	13	6
KH14	F	Adult	57	Migrant	22 May 2008	VHF	8	45
KH15	F	Yearling	42	Resident	23 May 2008	VHF	25	108
KH16	M	Fawn	37	Dispersal/migrant	27 May 2008	VHF	20	66
KH17	F	Adult	53	Migrant	28 May 2008	VHF	25	99
KH18	F	Adult	54	Migrant	8 July 2008	GPS+VHF	24	875

(continued)

Table 10.1 (continued)

Deer ID	Sex	Age	Body mass (kg)	Movement strategy	Date of capture	Collar type	Tracking period (months)	Number of fixes
KH19	F	Adult	53	Migrant	9 July 2008	VHF	24	94
KH20	M	Adult	105	Migrant	9 July 2008	GPS+VHF	8	4296
KH21	F	Adult	56	Migrant	23 July 2008	GPS+VHF	19	8905
KH22	F	Adult	63	Resident	12 May 2010	GPS	12	1348
KH23	F	Adult	55	Migrant	20 May 2010	GPS	12	13,490
KH24	F	Adult	50	Migrant	4 August 2010	GPS	11	6396
KH25	F	Adult	52	Migrant	21 April 2011	GPS	17	9537
KH26	F	Adult	57	Migrant	20 May 2011	GPS	16	8185
KH27	F	Adult	56	Resident	24 May 2011	GPS	13	6419
SA1	M	Adult	63	Migrant	26 October 2007	GPS	12	3001
SA2	M	Adult	92	Resident	6 October 2008	GPS	10	3005
SA3	F	Adult	52	Migrant	28 September 2009	GPS	12	6518
SA4	M	Adult	95	Migrant	3 October 2009	GPS	12	7497
SA5	M	Adult	75	Migrant	10 October 2009	GPS	9	5134
SA6	M	Adult	66	Migrant	10 October 2009	GPS	12	5072
SA7	M	Adult	55	Migrant	3 June 2010	GPS	12	6278
SA8	M	Adult	65	Migrant	4 October 2010	GPS	10	6926
SA9	M	Adult	89	Migrant	11 October 2010	GPS	12	7559
SA10	F	Adult	55	Migrant	16 October 2007	GPS	11	7470

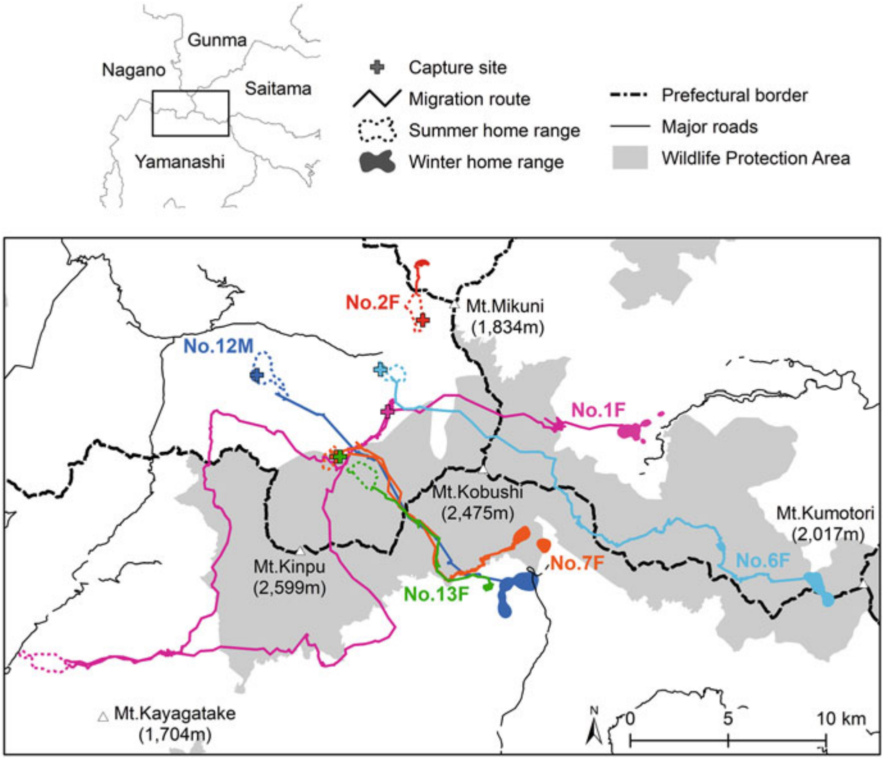

Fig. 10.2 Seasonal home ranges and migration route of six GPS-collared sika deer in the Okuchichibu Mountains. Deer were captured at Kawakami Village, Nagano, in spring 2009

10.4.1.2 Migratory Movement

All the migrants migrated between distinct summer and winter home ranges. In addition to these two seasons, six male deer in the Southern Japan Alps had distinct autumn and spring home ranges. The median start date of autumn migration (departure date from the summer home range) differed significantly between three study areas ($\chi^2 = 12.805$, $p = 0.0017$). The median start date was earliest in the Southern Japan Alps (7 September) and latest in the Kirigamine Highland (23 November) (Table 10.2). The duration of autumn migration was 6.1 ± 5.3 days (0.3–12.6 days, $n = 6$) in the Okuchichibu Mountains, 2.2 ± 0.5 days (1.6–2.8 days, $n = 5$) in the Kirigamine Highland (GPS-collared deer), and 2.9 ± 1.9 days (1.0–6.8 days, $n = 7$) in the Southern Japan Alps ($\chi^2 = 1.805$, $p = 4.056$). The median arrival date on the summer home range was earliest in the Kirigamine Highland (31 March) and latest in the Southern Japan Alps (10 June). The mean arrival date was 71 days later in the Southern Japan Alps ($z = -4.256$, $p = 0$). The duration of spring migration was 3.2 days ($n = 1$) in the Okuchichibu Mountains, 1.4 ± 0.9 days (0.2–2.4 days, $n = 4$) in the Kirigamine Highland (GPS-collared deer), and 40.2 ± 23.9 days (4–69 days,

Table 10.2 Migration distance, median date of autumn and spring migration, and seasonal home range in the three study areas

Migratory type		Okuchichibu Mountains	Kirigamine Highland	Southern Japan Alps
Migrants	*n* (female, male)	5, 1	14, 3	2, 7
	Migration distance (range)	15.8 ± 10.9 km (2.5–31.9)	9.9 ± 5.7 km (3.2–22.9)	13.0 ± 5.8 km (3.4–22.6)
	Autumn migration date (*n*)[a]	25 October (6)	23 November (27)	7 September (7)
	Range	17 September–3 November	27 August–1 January	7 August–29 October
	Spring migration date (*n*)[b]	10 April (2)	31 March (23)	10 June (9)
	Range	23 March–29 April	27 February–26 May	9 May–5 July
	Summer home range: female (*n*)	5	14	2
	95% FKD (range)	98 ± 32 ha (54–141)	348 ± 380 ha (29–1239)	133 ha (79–188)
	Winter home range: female (*n*)	5	5	2
	95% FKD (range)	36 ± 42 ha (15–111)	307 ± 308 ha (17–701)	80 ha (40–120)
	Summer home range: male (*n*)	1	2	7
	95% FKD (range)	180	688 ha (413–962)	106 ± 76 ha (20–227)
	Winter home range: male (*n*)	1	0	7
	95% FKD (range)	217	–	145 ± 103 ha (36–341)
Residents	*n* (female, male)	–	6, 3	0, 1
	Summer home range: female (*n*)	0	6	0
	95% FKD (range)	–	355 ± 486 ha (53–1426)	–
	Winter home range: female (*n*)	0	2	0
	95% FKD (range)	–	119 ha (87–151)	–
	Summer home range: male (*n*)	0	2	1
	95% FKD (range)	–	1177 ha (339–2014)	306
	Winter home range: male (*n*)	0	0	1
	95% FKD (range)	–	–	90

[a] Median of departure date from summer home range

[b] Median of arrival date of summer home range

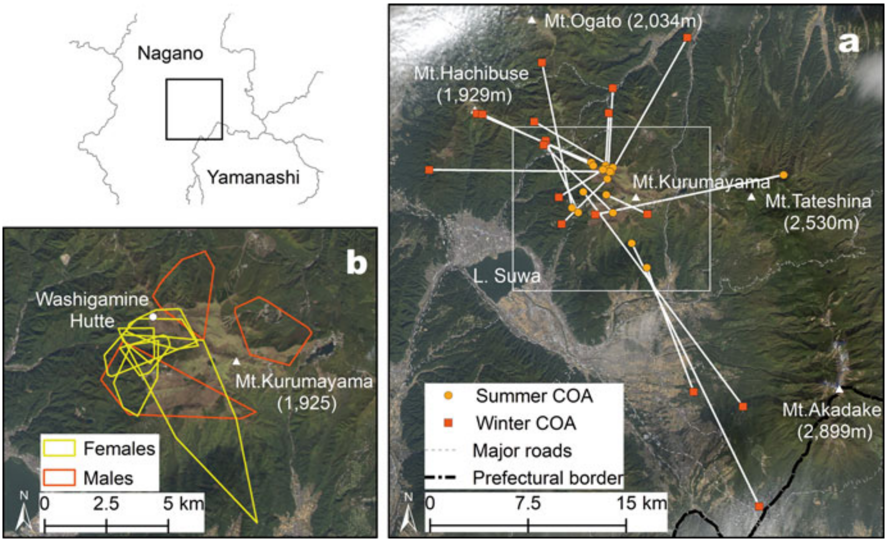

Fig. 10.3 Summer and winter center of activity (COA) with a connected line, which indicates distance and direction for 17 (14 females and 3 males) migrants in Kirigamine Highland, 2008–2011 (**a**). Annual home ranges of eight residents (six females and two males), 2008–2012 (**b**). The area of (**b**) is outlined as a square in (**a**)

$n = 8$) in the Southern Japan Alps. The duration of spring migration was significantly longer than autumn migration in the Southern Japan Alps ($z = -2.201$, $p = 0.0277$).

The mean migration distance between the summer and the winter home range (9.9–15.8 km) was not significantly different among three study areas ($\chi^2 = 2.604$, $p = 0.2720$). A female deer in the Okuchichibu Mountains exhibited the longest migration distance of 31.9 km.

In the Okuchichibu Mountains, five deer stayed in Kawakami Village (capture area) during the summer, whereas one female stayed in Yamanashi Prefecture, 21.6 km southwest from the capture site (Fig. 10.2). All the deer wintered outside the Kawakami Village, and the autumn migration route crossed a high divide of the Okuchichibu Mountains, which is also the prefectural border. Two out of five female deer had two distinct winter home ranges (38–100< days at each range). The deer initiated autumn migration earlier than 12 days before the hunting season (17 September–3 November, $n = 6$) and departed from the winter home range during March (3–28 March, $n = 5$).

In the Kirigamine Highland, 16 out of 17 migrants moved from the Kirigamine Highland to contiguous areas with various directions to winter, whereas 3 deer wintered at the foothills of the Yatsugatake Mountains (Fig. 10.3). Only one migrant male summered near Mt. Tateshina (2530 m a.s.l.) and wintered at the Kirigamine Highland. The deer initiated autumn migration from 27 August–1 January and arrived in the Kirigamine Highland during 27 February–26 May.

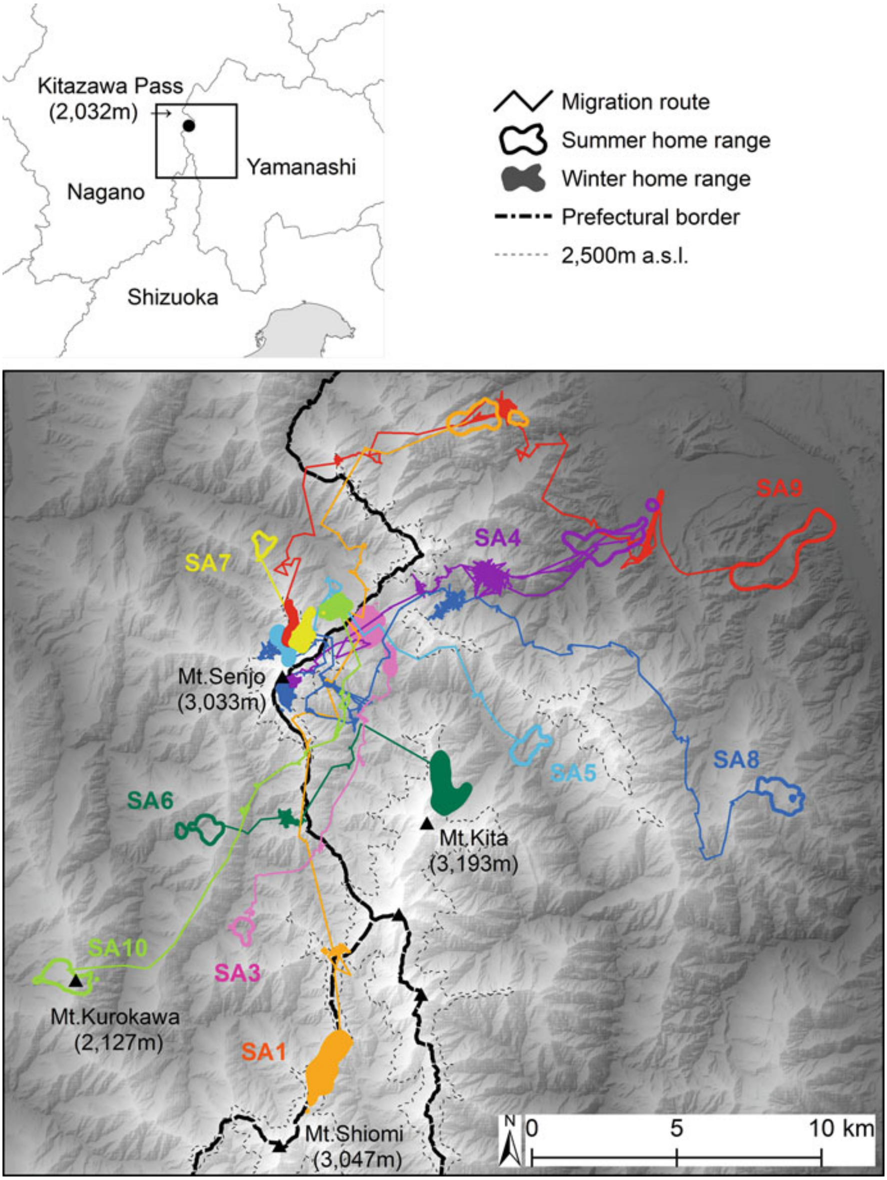

Fig. 10.4 Seasonal home ranges and spring migration route of nine migrants (two females and seven males) in the Southern Japan Alps, 2007–2012. The migration route of SA7 is the autumn migration route

In the Southern Japan Alps, two female migrants stayed near the capture site during the summer and migrated southwest to winter, whereas seven male migrants moved to the alpine zone during the summer and moved to various directions except

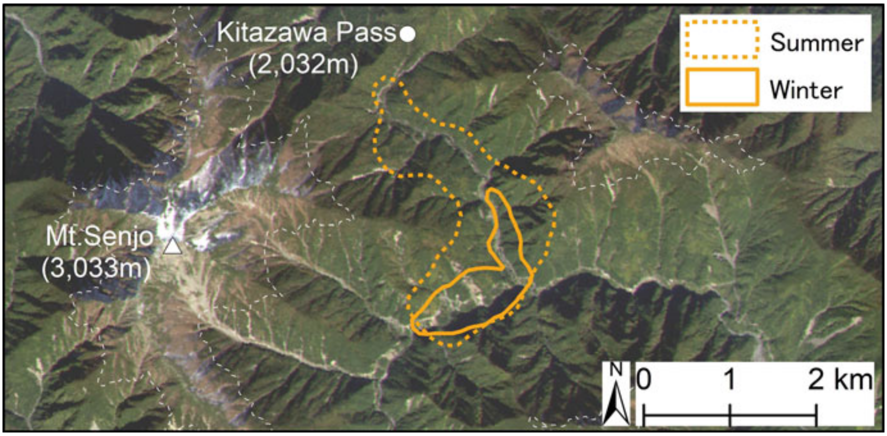

Fig. 10.5 The summer and the winter home range (fixed kernel) of resident male deer in the Southern Japan Alps, 2008–2009. The dashed white line shows the altitude of 2500 m

south to winter (Fig. 10.4). Two female migrants initiated autumn migration during 12–29 October, whereas male migrants initiated autumn migration during 7 August–28 September. Eight out of 9 migrants arrived at the summer home range during 3 June–5 July, whereas one female arrived on 9 May.

10.4.1.3 Seasonal Home Range

Home range size. We were only able to compare the female's summer and winter home ranges in the Okuchichibu Mountains and the Kirigamine Highland (Table 10.2). Both summer and winter home range sizes were not significantly different between these two study areas (summer FKD: $z = 0.463$, $p = 0.6434$; winter FKD: $z = 1.786$, $p = 0.074$). Although there were less than two deer data on the winter home range size of residents, winter home range size was smaller compared to winter at the Kirigamine Highland and the Southern Japan Alps. The summer home range of migrant and resident females did not differ significantly (Kirigamine Highland, FKD: $z = 0.247$, $p = 0.8046$). Furthermore, in the Okuchichibu Mountains, the winter home range was significantly smaller than in the summer ($z = 1.997$, $p = 0.0459$), and there were no significant differences between the summer and the winter in other study areas.

Fidelity to the seasonal home range. In the Kirigamine Highland, all the deer monitored for ≥ 2 seasons (summer: $n = 15$; winter: $n = 13$) had overlapping summer and winter home ranges. The distance between the COA of successive summer and winter home range was greater during the winter (768 ± 623 m, $n = 13$) than during the summer (403 ± 536 m, $n = 27$), indicating high fidelity to the summer home range ($z = -2.122$, $p < 0.05$).

Elevation. Regarding the migrants, the summer elevation was significantly higher than the winter home range at two study areas (Table 10.3; Kirigamine Highland: $z = 2.769$, $p = 0.0056$; Southern Japan Alps: $z = 2.666$, $p = 0.0077$), but it was not significantly different in the Okuchichibu Mountains ($z = -0.105$, $p = 0.9165$). Besides, the summer elevation significantly differed among three study areas ($\chi^2 = 19.395$, $p = 0.0001$), whereas the winter elevation was not significantly different ($\chi^2 = 3.484$, $p = 0.1752$). The mean summer elevation in the Southern Japan Alps (2486 m) was significantly higher than the other two study areas (Kirigamine Highland: $z = -4.123$, $p = 0$; Southern Japan Alps: $z = -3.182$, $p = 0.0015$). In the Southern Japan Alps, seven males demonstrated a remarkable altitudinal difference between summer and winter home ranges (780–2052 m), and they summered in the alpine zone (>2400 m a.s.l.) and wintered in montane to subalpine zone (744–1778 m). Meanwhile, two migratory females utilized subalpine zone throughout the year with small altitudinal differences (20−276 m). Resident deer at the Kirigamine Highland used higher elevation in the summer compared to the winter ($z = 2.31$, $p = 0.0209$). A resident male deer at the Southern Japan Alps utilized a mean elevation of 1911 m during the summer, and 1879 m during the winter. There were only four deer that wintered >1800 m a.s.l. in three study areas.

Coniferous cover. The percentage of coniferous cover in the winter home range was significantly higher than the summer home range, only in the Okuchichibu Mountains (Table 10.3, $z = -2.201$, $p = 0.0277$). The migratory deer in the Southern Japan Alps showed a higher percentage of coniferous cover than the Kirigamine Highland during the winter ($z = -2.2$, $p = 0.0278$).

Topography. The percentage of southerly aspects in the winter home range was significantly higher than the summer home range, only at the Okuchichibu Mountains (Table 10.3, $z = -2.201$, $p = 0.0277$). There were no significant differences between the percentage of southerly aspects among three study areas in both seasons (summer: $z = 2.857$, $p = 0.2397$; winter: $z = 0.552$, $p = 0.7589$). The percentage of steep slope in the winter home range was significantly higher than the summer in the Okuchichibu Mountains ($\chi^2 = 1.023$, $p = 0.5995$) and the Kirigamine Highland ($z = -2.023$, $p = 0.0431$). Although steep slope ratio in the winter home range did not significantly differ among the three study areas ($\chi^2 = 1.023$, $p = 0.5995$), it significantly differed during the summer ($\chi^2 = 14.621$, $p = 0.0007$). In the summer home range, the deer in the Kirigamine Highland exhibited the lowest steep slope ratio compared to the other study areas (Okuchichibu Mountains: $z = -2.714$, $p = 0.0066$; Southern Japan Alps: $z = -3.334$, $p = 0.00009$).

Road density. The road density in the winter home range greatly declined compared to the summer, only in the Okuchichibu Mountains (Table 10.3, $z = -2.201$, $p = 0.0277$). Although road density in the winter home range did not significantly differ among the three study areas ($\chi^2 = 0.556$, $p = 0.7575$), it significantly differed during the summer ($\chi^2 = 7.238$, $p = 0.0206$). The road density in the summer home range was higher in the Okuchichibu Mountains compared to the other study areas (Kirigamine Highland: $z = -2.289$, $p = 0.0221$; Southern Japan Alps: $z = 2.36$, $p = 0.0183$).

Table 10.3 Elevation, southerly aspects, steep slope, coniferous cover, and road density of the seasonal home range of migrants and residents in the three study areas

		Okuchichibu Mountains					Kirigamine Highland					Southern Japan Alps				
	Migratory type	Summer		Winter			Summer		Winter			Summer		Winter		
Characteristics		Mean	*SD*	Mean	*SD*	*P*	Mean	*SD*	Mean	*SD*	*P*	Mean	*SD*	Mean	*SD*	*P*
Elevation (m)	Migrants	1486	285	1538	178	0.92	1605	114	1378	271	0.01	2486	316	1517	417	0.01
	Residents	–		–		–	1590	103	1516	81	0.02	1911		1879		–
Southerly aspects ratio (%)	Migrants	9	9	29	21	0.03	19	11	37	17	0.08	15	15	27	23	0.17
	Residents	–		–		–	16		26		–	16		62		
Steep slope ratio (%)	Migrants	34	11	61	14	0.03	12	9	49	16	0.04	61	23	61	26	0.95
	Residents	–		–		–	3		14		–	80		61		
Coniferous cover ratio (%)	Migrants	8	19	20	28	0.03	13	15	15	22	0.69	33	31	44	34	0.21
	Residents	–		–		–	9		32		–	84		54		
Road density (m/ha)	Migrants	14.2	6.3	1.0	2.4	0.03	5.1	5.0	8.0	10.1	0.74	4.1	8.5	5.3	10.7	0.9
	Residents	–		–		–	23.9		10.4		–	34.8		0		

10.4.2 Dispersal: A Case Study in Kirigamine Highland

We observed dispersals for all four VHF-collared male fawns captured at the Kirigamine Highland (Fig. 10.6, Table 10.4). The deer were 12- to 23-month-old

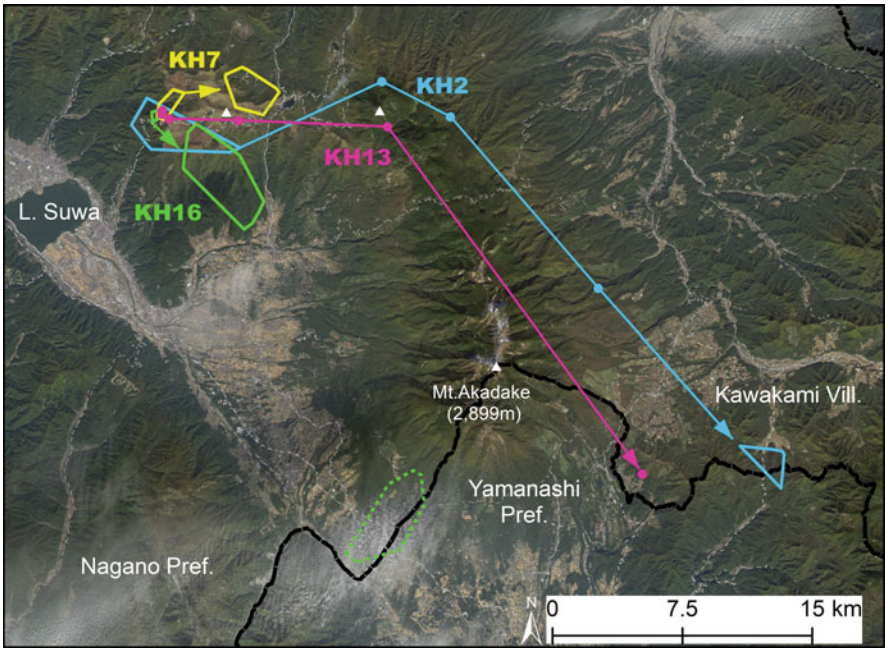

Fig. 10.6 Pre-dispersal and postdispersal home range (100% minimum convex polygon) of four juvenile male deer captured in the Kirigamine Highland, Nagano, 2008. The arrow indicates the direction of dispersal. Deer KH16 exhibited migratory movements between summer (solid line) and winter home range (dotted line). The dashed grey line shows the major roads

Table 10.4 Dispersal age, date, distance, and postdispersal migration pattern of four juvenile male sika deer captured in Kirigamine Highland, Nagano, central Japan, 2008

Deer ID	Body mass (kg)	Age (months)		Dispersal[a] date	Dispersal distance (km)	Postdispersal migration pattern
		Capture	Dispersal			
KH2	36	10	23	14 May 2009	40.3	Resident
KH7	26	11	17	13 Nov 2008	4.3	Resident
KH13	35	11	12	16 Jun 2008	34.6	Unknown[b]
KH16	37	11	12	18 Jun 2008	3.0	Migrant

[a] The date when dispersal began
[b] The deer was killed in August 2009

when dispersal initiated. Three deer dispersed during May and June, whereas one deer dispersed in November. Dispersal distance ranged from 3.0 to 40.3 km. From visual observation and radio-tracking, two male fawns belonged to their mothers' group that we had radio-tracked during the pre-dispersal period. Both fawns exhibited nonmigratory movement following the dispersal, which was the same as their mother's movement patterns.

10.5 Discussion

10.5.1 Comparison of Movement Characteristics Among Three Regions

10.5.1.1 Movement Pattern

We determined the movement pattern of 43 deer (27 females and 16 males) in 3 study areas, and we observed both migrant and resident deer (partial migration) in the Kirigamine Highland and the Southern Japan Alps. We were unable to track resident deer in the Okuchichibu Mountains, possibly because of the small sample size. Furthermore, this study is the first to describe sika deer migration using >20 individuals in central Honshu. The partial migration of sika deer in Japan has been indicated in a few studies (Maruyama 1981; Takatsuki et al. 2000; Igota et al. 2004), whereas it has been well documented in other cervid populations (e.g. Kufeld et al. 1989; Mysterud 1999; Sabine et al. 2002; Cagnacci et al. 2011). The mixed-migration pattern of deer in the same area had been explained by climate variability, especially snow depth (Nicholson et al. 1997; Brinkman et al. 2005; Ramanzin et al. 2007). Borkowski et al. (1996) reported that sika deer used westerly exposures with less snow cover as the snow deepened in the winter. The proportion of migrants was higher than that of residents, both in the Kirigamine Highland and the Southern Japan Alps, and these areas were snowy due to high elevation. It has been reported that in the less snowy region, the proportion of residents is higher than that of migrants (Kufeld et al. 1989), whereas in the snowy region, migratory deer dominate in the population (Garrot et al. 1987; Nicholson et al. 1997). Although we were able to analyze the seasonal home range of only two resident deer in the Kirigamine Highland, these deer had a higher percentage of southerly aspects and steep slopes in the winter home range. We assume that the rugged terrain in these study areas, which hold various aspects and slope gradients, provided various snow cover patterns. Such variable winter conditions probably enabled the nonmigratory deer to winter in these areas. On the other hand, we observed that deer were also migratory in the less snowy region (Okuchichibu Mountains), and the driving force of the migratory movements in this area may be different from the other two areas.

Notably, we observed a resident male deer at ca. 1900 m a.s.l. of the Southern Japan Alps. This deer had a smaller home range in the winter compared to the summer, and the winter home range was located along the forest road (Fig. 10.5).

During the construction of the forest road in this area, an artificial grassland was created as slope revegetation works, which provided high-quality forage. The deer was able to overwinter, probably due to the abundant forage and available shelter (evergreen coniferous forests) from heavy snow. The artificial grassland in this area comprises evergreen foreign pasture grass (Hatakeyama 1979), and deer mostly prefer this vegetation (Mitani et al. 2005). Furthermore, forage availability along the forest road area is abundant compared with forests (Terada et al. 2010). Evergreen coniferous forests dominating the surrounding area also provide shelter from the heavy snow during the winter (Igota et al. 2004). Thus, forest roads may be a key factor for the partial migration strategy in this area.

10.5.1.2 Migratory Movement

The mean migration distances in the three study areas were not significantly different (9.9−15.8 km). Sika deer in Hokkaido have been known to migrate long distances (Uno and Kaji 2000; Igota et al. 2004), while in Honshu, sika deer are thought not to migrate long distances due to fragmented habitat (Yabe and Takatsuki 2009). Compared with Hokkaido, where deer exhibit large-scale migrations (Igota et al. 2009), the heavy snow region is limited to areas along the Sea of Japan and the subalpine to alpine ranges in central Japan (Japan Meteorological Agency 2002). From 2008 to 2011, the maximum snow depth at Washigamine Hütte in the Kirigamine Highland ranged from 56 to 108 cm, whereas at the Suwa meteorological station (36°03'N, 138°07'E; 760 m a.s.l.), ca. 11 km southwest of Mt. Kurumayama, the maximum snow depth only ranged from 11 to 22 cm (Meteorological data of Nagano Prefecture, Nagano Local Meteorological Observatory, Nagano). The migration patterns of elk (*C. canadensis*: Dalke et al. 1965) and mountain goat (*Oreamnos americanus*: Rice 2008) exhibit substantial altitudinal differences, but they have shorter horizontal migration distances, which might be consistent with the case of our study. Thus, it is likely that sika deer may not need to travel long distances to seek wintering areas in central Japan. A female deer in the Okuchichibu Mountains exhibited the longest migration distance of 31.9 km. The extensive areas of uncultivated land in the Okuchichibu Mountains made it possible for deer to migrate such long distances.

10.5.1.3 Driving Force of Migration

Comparing the characteristics of the seasonal home ranges, the driving forces of migration were different in the three study areas.

The Okuchichibu Mountains were different from other study areas because the deer summered in less snowy areas, and it was the only study area where the elevation of the seasonal home range did not significantly differ. The maximum snow depths in the summer home ranges were 17 to 43 cm, whereas in the winter it was 28 to 37 cm (Japan Meteorological Agency 2002). Considering the small elevation difference between the summer and the winter home ranges and relatively small snowfall in the study area, snow was less likely the driving force of departure from the summer home range. Human activity is also one of the factors that influence autumn migration. The deer utilized areas with very low road density (1.0 m/ha) in the winter compared to the summer (14.2 m/ha), which indicates that deer migrated to areas with less anthropogenic effects. All the deer's summer home ranges were within the hunting zone, and the departure date of the summer home range was earlier than 12 November, which was 3 days before the start of hunting season (15 November). Furthermore, a total of 874 deer were harvested in Kawakami Village during the summer of 2009, whereas 5 out of 6 deer wintered in areas with low hunting pressure (<10 deer/5 km^2, during the winter) (Takii et al. 2012a). Although one female deer (OM2) wintered in an area with relatively high hunting pressure (56 deer/5 km^2), hunting did not take place at her winter home range (H. Nakayama, pers. comm.). These results may indicate that the deer wintered in places with less anthropogenic effects.

In the winter home range, the proportion of coniferous cover, southerly aspects, and steep slopes was higher than in the summer. It is best for deer to remain undisturbed to minimize unnecessary energy loss (Moen 1976). Furthermore, in general, coniferous cover, southerly aspects, and steep slope areas are shallower in snow depth. Winter forage is another factor that influences autumn migration. The critical winter forage for the sika deer inhabiting central to northern Honshu is bamboo grass (Furubayashi and Maruyama 1977; Takatsuki 2009), which has the highest crude protein content and forage availability during winter (Yamane 1999). Igota et al. (2004) revealed that the variety of bamboo grass contributed to the migration patterns of sika deer. Bamboo grass (*Sasamorpha borealis* or *Sasa hayatae*) was absent in the summer home range, whereas bamboo grass was dominant in the winter core area (Takii et al. 2012a). Thus, we conclude that the deer wintered in areas with less human activity, abundant winter forage, and less snowy areas to minimize energy expenditures during the winter.

The autumn migration date (departure date from the summer home range) was the latest in the Kirigamine Highland (23 November, Table 10.2). In this study area, snow depth was recorded daily at Washigamine Hütte (1660 m a.s.l.). From observing the departure date of individual deer from the summer home range in 2 consecutive years, $>80\%$ of the deer migrated before the snow depth reached >20 cm in both years, and the number of days with snow depth >40 cm were 22 and 60 during these years (Takii et al. 2012b). Thus, autumn migration in the Kirigamine Highland occurred before the snow depth reached 20 cm, far below the point known to prevent the sika deer locomotion (50 cm: Takatsuki 1992). Besides snow, 50–100% of autumn migration occurred after the daily temperatures $< 0°C$ persisted for more than 3 days (Takii et al. 2012b). These results were consistent with previous studies indicating that severe winter weather (i.e., deep snow and freezing temperatures) influences the onset of autumn migration (Nelson 1995; Nicholson et al. 1997; Mysterud 1999; Sabine et al. 2002; Brinkman et al. 2005; Grovenberg et al. 2009; Monteith et al. 2011). Deep snow limits the movement and increases the energy expenditures of deer (Parker et al. 1984); moreover, snow cover reduces a significant amount of available forage during the winter (Schwartz and Hobbs 1985). Furthermore, heat loss is greater in low ambient temperatures (Moen 1968), especially when the quality and quantity of forage are limited. Therefore, deer are likely to migrate from the Kirigamine Highland to minimize energy costs because deep snow limits forage availability and locomotion.

The mean arrival date to the Kirigamine Highland was 31 March. Fifty to 75% of the deer had arrived after the snow disappeared, and the remaining deer arrived when snow depths were rapidly decreasing (Takii et al. 2012b). In addition, all the deer arrived at the summer home range, after >0°C persisted for more than 3 days (Takii et al. 2012b). Thus, spring migration in the Kirigamine Highland was associated with increasing temperatures and occurred when either snow had disappeared entirely or during the rapid melting period. These results were consistent with previous findings (Nelson 1995; Uno and Kaji 2000; Sabine et al. 2002; Igota et al. 2004; Brinkman et al. 2005; Ramanzin et al. 2007). The duration of the spring migration (52–74 days) was shorter than that of the autumn migration (123–127 days), which is consistent with the results of white-tailed deer (*Odocoileus virginianus*) (Sabine et al. 2002). Meanwhile, since plant growth is arrested during the winter, the longer the stay of deer in the winter range, the more limited the food availability. Monteith et al. (2011) showed that it is beneficial for the deer to leave the winter range as early as possible to seek better forage, explaining our results. Sakuragi et al. (2003) revealed that north migrants feed more on high-quality forage than nonmigrants during summer. Although data on forage quality is lacking, spring migration may be attributed to the extensive grasslands in the Kirigamine Highland. Sika deer in northern Japan are highly dependent on graminoids and are identified as grazers (Takatsuki 2009). Furthermore, high fidelity to the summer home range corresponded to earlier studies of sika deer (Uno and Kaji 2000; Igota et al. 2004) and other cervids (Tierson et al. 1985; Nicholson et al. 1997; Van Deelen et al. 1998). Such strong fidelity to summer ranges indicates high fidelity to breeding sites for females. Because reproduction (i.e., pregnancy and lactation) is energetically expensive (Oftedal 1985), deer must feed on high-quality diets from spring to autumn. Thus, extensive grassland will provide a favorable habitat for sika deer during the summer.

In contrast to the Kirigamine Highland, the autumn migration date (departure date from the summer home range: 7 September) was the earliest, and the spring migration date (arrival date at the summer home range: 10 June) was the latest at the Southern Japan Alps (Table 10.2). Seven out of 9 migrants' summer home ranges were in the alpine zone (alpine deer).

Alpine plants initiate plant growth when air temperatures reach above 5°C (Kudo and Suzuki 1999; Wipf 2010). Although the estimated air temperature at 2500 m a.s.l. reached 5°C during 3–10 May, the first day that >5°C persisted for more than a week was during 3–11 June, and all the deer started to stay >2500 m a.s.l. from 3 June to 5 July (Takii 2013). At 2900 m a.s.l. of Mt. Kita, Natori (2008) documented that the first day when the daily air temperature recorded 5°C was 1 June and the plants' growing period persisted for 4 months. The first date when the estimated air temperature reached below 5°C was 23–27 September during the study period, and deer that stayed in the alpine zone departed from the summer home range from 7 August to 28 September (Takii 2013). Hence, the alpine deer is considered to stay in the alpine zone from the early to the end of the plant's growing period.

The mean duration of the spring migration was 40.2 days in the Southern Japan Alps, which was ca. 14 times longer than the autumn migration. The spring migration proceeded slower than in autumn, probably to access high nutrient forage. Crude protein content and plant digestibility are usually high during the early growing season (Johnston et al. 1968; Van Soest 1994; Hebblewhite et al. 2008). Several studies revealed that deer have spring home ranges (Morgantini and Hudson 1989; Kucera 1992), where the quality of forage plants is high (Morgantini and Hudson 1989). Migratory deer may be moving slowly along with plant phenological stages to access early growing plants (Mysterud et al. 2011). Contrarily, all the alpine deer initiated autumn migration before snowfall in the alpine zone (the first snowfall was mid-October for 2009–2011, according to the notes from the mountain lodge at Mt. Senjo). All the alpine deer were male and had autumn home ranges. Considering that the breeding season of sika deer starts in September, the alpine deer's autumn migration is considered a response to the shortage of food availability and the movement toward the breeding area.

10.5.2 Dispersal

Few studies have reported the dispersal of sika deer in Japan (Maruyama 1981; Yamazaki and Furubayashi 1995; Takii et al. 2012b; Takii et al. 2019). We found that age, date, and dispersal distance varied among individuals; however, this may be due to the small sample size. Although Yamazaki and Furubayashi (1995) reported that one yearling male deer initiated dispersal when it was 2.5 years old, we found that males had dispersed at younger ages. In white-tailed deer, $\geq$50% of juvenile males disperse, but the dispersal age ranged from 10 to 30 months (DeYoung 2011), which coincided with our results. A male fawn (KH2) that dispersed 40.3 km southeast from the Kirigamine Highland became a resident deer in the neighboring mountain, at the western end of the Okuchichibu Mountains. Takii et al. (2019) described the dispersal movement of a male fawn with GPS telemetry at the foothills of the Northern Japan Alps that dispersed 74 km. Although at the Kirigamine Highland, male sika deer exhibited the same philopatric movement as his mother, Takii et al. (2019) reported that the movement pattern differed from his mother. Further study with sufficient sample size is required to interpret the dispersals of sika deer.

10.6 Conclusion

We revealed that the deer exhibited partial migration in the mountainous region of central Honshu. Of the 43 deer analyzed, 32 (74%) were migrants, 10 (23%) were residents, and 4 were dispersers. The major topographical features of this area are continuous mountains with rugged terrain and large elevation differences, which provide variable winter conditions for deer to overwinter in the relatively high-elevation area. The migrants were dominant because most of the study areas were snowy due to high elevation, but as in the case of the Okuchichibu Mountains, snow may not always be the trigger of autumn migration.

Although the distance of migration varies depending on the habitat and terrain (Stewart et al. 2011), the mean migration distances of three areas (9.9–15.8 km) were not significantly different. The deer in this area may not need to migrate long distances (e.g., 35.1 km, Igota et al. 2004) due to the variety of altitudinal gradients. Furthermore, the complex terrain (steep slopes and deep valleys) provided wintering areas for deer. The steep terrain also provided shelter from anthropogenic effects (i.e., human hunting pressures); thus, winter refuges of deer were not limited to specific areas. There were 1 to 2 deer that exhibited migration distance >20 km in each study area. Such long distances had never been reported in the Honshu area, and we assume that the deer were able to migrate long distances due to the continuous mountainous areas.

Although the mean altitude in the summer home range differed between the study areas, the mean altitude in the winter did not differ. This indicates that migrants overwinter in a less snowy area of ca. 1300 to 1600 m a.s.l. Furthermore, it was common to the three study areas that most of the deer's winter home ranges did not overlap, and road density was low. There may be a wide range of refuges in the study area, where the deer can stay undisturbed during the winter.

For sika deer, the factors influencing autumn migration were reported to be snow avoidance (Maruyama 1981; Takatsuki et al. 2000; Igota et al. 2004), winter forage availability (Igota et al. 2004), and avoidance of hunting activities (Kamei et al. 2010). In this study, we described that the factors were different among the study areas. In the Okuchichibu Mountains, a less snowy region, high human hunting pressure and the low availability of winter forage (i.e., bamboo grass) in the summer home range were the key factors influencing autumn migration. In the Kirigamine Highland, a snowy grassland, most deer departed the grassland before the snow depth reached 20 cm, indicating that snow limited the movement and winter forage of deer. The autumn migration in the Southern Japan Alps also occurred before snowfall, but the departure dates were much earlier than the Kirigamine Highland. This is probably due to the short growing period of alpine plants.

Arrival dates to the summer home range in the Kirigamine Highland and the Southern Japan Alps coincided with the early growing period of plants. During the early growing period of plants, nitrogen and crude protein content increase with elevation (Körner 1989; Albon and Langvatn 1992). Since snowmelt is closely related to plant growth (Monteith et al. 2011), the deer migrated to the Kirigamine

Highland to access abundant forage in the vast grasslands and, in the Southern Japan Alps, to access the alpine vegetation from the most nutritious, early growing period. Notably, fidelity to the summer home range was stronger than the winter in the Kirigamine Highland. The strong fidelity to the summer home range indicates that grasslands in the Kirigamine Highland are an essential habitat that provides abundant forage during the summer. Thus, spring migration can be interpreted as a return movement to critical deer habitat (breeding area) (Cagnacci et al. 2011).

Although we were able to compare the female seasonal home ranges in the Okuchichibu Mountains and the Kirigamine Highland, and male home ranges in the Southern Japan Alps, only females in the Okuchichibu Mountains had significant differences between the summer and the winter. Deer in this area had smaller winter home ranges probably to avoid anthropogenic effects since the autumn migration was associated with hunting pressure. In addition, the wintering areas of this area were located at remote places in the mountains. The home range sizes are affected by sex, age, hiding place, or forage quality (Sanderson 1966; Brinkman et al. 2005). In severe winter areas, winter home ranges tend to be smaller than in the summer (Lesage et al. 2000; Igota et al. 2004). In our study area, the home range size had a wide range of variety even within sex, and we did not detect any differences between study areas. This might indicate the diversity of deer utilization patterns in the study area.

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Chapter 11
Movement Characteristics and Habitat Use of Sika Deer in Kanto Region, Central Japan

Tadanobu Okumura, Yukiko Namba, Zhao-Wen Jiang, Yusaku Yamada, and Yoshifumi Sugiura

Abstract We aimed to clarify the seasonal movement, activity range, and habitat use of sika deer (*Cervus nippon*) in Oze and Okuchichibu areas, including both plateau wetlands and forest ecosystems, Kanto region, central Japan, using GPS collars. We analyzed position data from 56 deer, 37 (5 males and 32 females) in Oze and 19 (6 males and 13 females) in Okuchichibu areas. We divided sika deer into three movement patterns as residents, seasonal migrants, and irregular migrants. The proportion of seasonal migrants was higher in Oze area (75.7%) than that in Okuchichibu (36.8%). Further, we divided seasonal migrants in Oze area into two types, i.e., with and without stopover sites on migration routes between summer and winter habitats, and found that sika deer using stopover sites spend same period in summer habitat, but the duration in winter habitat was shorter than deer without stopover. This is probably due to that they intend to intake energy efficiently by taking time along migration route in accordance with phenology. The overlap rate between wildlife protection area (where sports hunting is prohibited even in hunting season in winter) and the home range of migratory deer was higher in winter than that in summer in Okuchichibu area, and the snow depth in summer habitat was greater than that in winter habitat in Oze area. Therefore, snow depth in Oze area and hunting pressure in Okuchichibu areas should be the important cause for seasonal movement of sika deer.

T. Okumura (✉) · Y. Namba · Z.-W. Jiang
Tokyo Division, Wildlife Management Office Inc., Hachioji, Tokyo, Japan
e-mail: okumura@wmo.co.jp; namba@wmo.co.jp; jiang@wmo.co.jp

Y. Yamada · Y. Sugiura
ROOTS Inc., Isumi, Chiba, Japan
e-mail: yamada@roots-wl.com; sugiura@roots-wl.com

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11.1 Introduction

Range expansion of sika deer (*Cervus nippon*) in Japan has accelerated in the last few decades. Their distribution areas increased 1.7 times during the 25 years from 1978 to 2003 and 2.7 times during the 40 years from 1978 to 2018 (Ministry of the Environment 2021), respectively. Several factors are considered to have contributed to the expansion of the sika deer distribution. The natural environment includes the decrease in snow cover due to global warming and the planting of Japanese cedar (*Cryptomeria japonica*), Japanese cypress (*Chamaecyparis obtusa* var.) in lower elevation, and larch (*Larix kaempferi*) in the subalpine in wide areas for lumber production by cutting broadleaf forests under the forestation expansion policy that started around 1960. The change in social environment, i.e., the increase of abandoned cultivated farmland due to depopulated and aged human society in the rural areas, is also an important factor (Miura 2007).

In addition, the dramatic decreasing and aging of hunter population since the peak in the 1970s has resulted in the decrease of deer hunting (Kaji et al. 2010). In contrast to the decrease of firearm hunters, trap hunters are increasing (Ueda and Kanzaki 2006). This is because of the fact that more and more farmers start to use traps as a convenient way to capture deer for preventing crop damage. However, most farmers lack knowledge of hunting; it is difficult to expect that farmers should be responsible for population control of sika deer (Ueda and Kanzaki 2006).

On the other hand, the current expansion of deer distribution is considered as the result of the restoration in their former habitats (Kaji et al. 2000), since deer was widely inhabiting the plains areas during the Edo period (1603–1868 CE, Koganezawa 1989; Kaji et al. 2000; Furubayashi and Shinoda 2001). However, in recent years, deer have expanded distribution not only to plains but also to the areas of high elevation (Izumiyama and Mochizuki 2008). By expanding into higher elevation areas where sika deer have not inhabited or inhabited slightly, feeding could have a serious impact on the alpine vegetation and the rare plants in alpine ecosystems, which had been established under the conditions of absence or low density of sika deer (Nagaike 2012).

The seasonal migration of sika deer has been reported to range from a few to tens of kilometers in Hokkaido (Uno and Kaji 2000; Igota et al. 2004) and Kanto regions (Maruyama 1981; Homma 1995; Izumiyama and Mochizuki 2008) in Japan. Most of the migrations are altitudinal movements, moving to higher elevation in summer and lower in winter (Maruyama 1981; Takatsuki et al. 2000; Igota et al. 2004; Izumiyama and Mochizuki 2008), although the opposite movement was also reported in Hokkaido (Igota et al. 2004), the Okuchichibu Mountains (Takii et al. 2012a), and the Tanzawa Mountains (Chap. 12), central Japan, recently.

We collected the position data by fitting GPS collars to sika deer in two specific areas of Kanto region, central Japan. One is the Oze area (including the districts of Oze plateau wetlands and Nikko), where the sika deer distribution has been expanding into wetlands in the recent 30 years and has impacted wetland ecosystem by feeding. The other is the Okuchichibu area (Chichibu-Tama-Kai National Park, the closest national park to Tokyo, and surrounding area). We try to clarify characteristics of the seasonal movement, activity range (home range and core area), and habitat use of sika deer living in both Oze and Okuchichibu areas including both wetland and forest ecosystems, in Kanto region, central Japan.

11.2 Study Area

Oze area including the marshlands of both Ozegahara Plateau and around Lake Ozenuma with the surrounding mountains in Oze district, locate at the elevation around 1400 m on the border of Gunma, Fukushima, and Niigata prefectures, and the mountain forests in Nikko district (Fig. 11.1). Ozegahara Plateau is a marshland developed in the Oze Basin, and Lake Ozenuma is created by the damming of the headwaters of the Tadami River of the Agano River system at the elevation around 1650 m. Water supply is rich due to the heavy snow during winter and abundant rainfall during rainy season, and snow depth reaches around 3 m deep in winter. Oze district has a typical mountain climate, as it is located between the climate types of Sea of Japan and the Pacific. According to the weather station in Hinoemata Village, the closest meteorological observatory to Oze district, the annual precipitation is

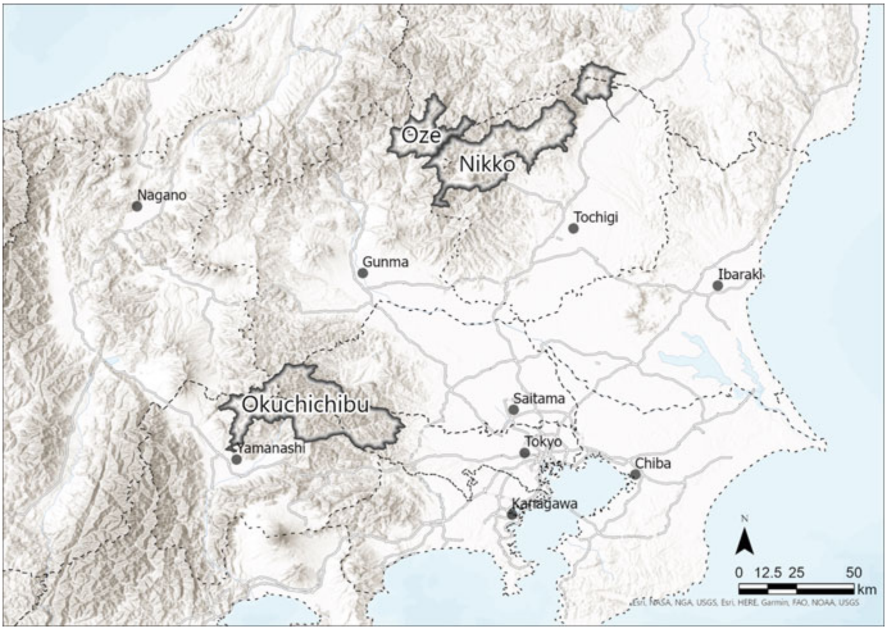


Fig. 11.1 The Kanto region showing the locations of the two study areas of Oze (including Oze and Nikko districts) and Okuchichibu, central Japan (all the background map from the open map source https://maps.gsi.go.jp/development/ichiran.html#english)

1560 mm, and the average temperature is −3.8 °C in January and 20.3 °C in August (30-year average from 1991 to 2020).

The volcanic high moor formed from the damming of a depression by ejecta from volcanic eruptions of the Oze volcanoes. At Ozegahara Plateau, in the lowland along the stream, Asian skunk cabbage (*Lysichiton camtschatcensis*) and marsh marigold (*Caltha palustris*) grow, as they prefer the flowing water environment. In places far away from the stream, there are oligotrophic environments in which nutrition is supplied only by the rainwater and specific wetland flora like Hare's tail cotton grass (*Eriophorum vaginatum*) and mosses (*Sphagnum* spp.) grow. The rare and valuable vegetation with many ponds resulted in a beautiful landscape and scenery in Oze distract and was designated as a part of Nikko National Park in 1934 and then was designated as Oze National Park in 2007 independently. The marshlands of Oze area were registered in Ramsar wetlands in 2005.

The occurrence of deer in the marshlands in Oze district was first reported in the 1980–1990s (Naito and Kimura 1998; Maruyama 2000) based on the observation of vegetation damage on altherbosa and Asian skunk cabbage by feeding, trampling, and even digging (Igarashi and Takatsuki 2008). It was believed that those deer inhabited the marshlands of Oze district only during summer due to the deep snow in winter, but there was no information for their winter habitat. Genetic analysis later proved that they originated in Nikko district of Tochigi Prefecture and Katashina Village of Gunma Prefecture (Koganezawa and Fukui 2003). In Nikko district, the deer expanded their range and increased the population size dramatically in 1980s because of decreasing snow, especially at higher elevations (Homma 1995; Li et al. 1996, 2001).

Okuchichibu area is located within the boundary area of five prefectures of Gunma, Saitama, Tokyo, Nagano, and Yamanashi, and the central part is designated as Chichibu-Tama-Kai National Park in 1950 (Fig. 11.1). The main ridge, the core area of Chichibu-Tama-Kai National Park, is lofty and has many deep valleys with steep slopes. The highest peak is Mt. Kita-Okusenjo at 2601 m in elevation, and snow depth reaches 1–2 m at main ridges in winter. The natural forests include deciduous broad-leaved primary forest with Japanese blue beech (*Fagus japonica*), Japanese beech (*Fagus crenata*), and Oak (*Quercus crispula*) in the lower zone around 600–1600 m in elevation and a coniferous forest at the subalpine dominated by Northern Japanese hemlock (*Tsuga diversifolia*), Maries' fir (*Abies mariesii*), and Erman's birch (*Betula ermanii*) in the higher area over 1600 m in elevation (Shigyo et al. 2017). Ohashi et al. (2014) reported the impact to natural vegetation caused by sika deer in 1990s first, and in the following decade, the impact expanded rapidly and became serious. In addition, the population increase of sika deer has caused dieback of Maries' fir and a severe decline of broad-leaved bamboos.

Okuchichibu area is long from east to west. The annual precipitation ranges from 1375 to 1432 mm, and the average temperature ranges from −5.8 to 1.8 °C in January and from 19.5 to 25.5 °C in August (30-year average for the period 1991–2020, Nobeyama weather station in the west and Chichibu weather station in the east part of Okuchichibu area).

11.3 Capture and Immobilization

We used a tranquilizer gun to capture and immobilize sika deer. We estimated the body weight to confirm the suitability for fitting GPS collar when we encountered sika deer and then injected the anesthetic to suitable deer as quick as possible. For immobilization, a mixture of ketamine and xylazine was used and atropine was added to minimize the side effects.

Under anesthetic condition, we measured body size and fitted a GPS collar. Then we injected suitable atipamezole as an antagonist to help the individual awake smoothly. We were keeping observation until the deer lifted its head and walked away healthily. To avoid the deer to have myopathy by excessive stress, we handled them carefully during capturing and collar fitting process to minimize stress (Suzuki 1999).

We used the GPS collars (GPS Plus and Vertex Plus series, Vectronic Aerospace GmbH, Germany) to track the movement of sika deer. We set a positioning schedule as 1–2-h intervals. The total weight of the GPS collar is about 800 g, and considering animal welfare, we fit the collars to deer ensuring the collar weight is less than 3% of the body weight.

11.4 Data Analysis

We obtained position data from GPS collars collected from the field after the end of the tracking period. The position data were displayed in the Geographic Information System (GIS), and any position data that were clearly outliers were removed by visual judge (D'Eon and Serrouya 2005). Referring to the plant phenology in the study area, the winter was defined as December through February, spring as March through May, summer as June through August, and autumn as September through November. Only individuals that had more than 30 days and over 100 position data within one season were used for analysis.

We analyzed the movement pattern, activity range (home range and core area), migration route, vegetation use, and the relationship among activity range, migration destination, and land use regulation, i.e., wildlife protection area or hunting permit area, using position data.

We calculated the activity range by ad hoc of Kernel method (Pellerin et al. 2008) of Adehabitat from R package (Calenge 2006) for all sika deer. We defined the 90% of the range as home range and 50% of the range as core area (Worton 1989).

We classified the movement pattern according to the status of overlap of seasonal home ranges and the seasonality of migration of each sika deer. We classified the sika deer with separate summer and winter home ranges and who migrate depending on season regularly as seasonal migrant (migratory) and that migrate not depending on season as irregular migrant. The sika deer with overlapped summer and winter home ranges were categorized as residents (sedentary). Further, we confirmed the home range forming on migration route between summer and winter habitats. We defined the seasonal migratory sika deer with small home range in certain sites on the migration routes and who stay multiple days in the home range as a type of seasonal migratory sika deer with stopover.

The timing and route of migration should have a large impact on the activity range. For further seasonal analyses, we focus on the seasonal variations of four seasons for sedentary sika deer only. And for seasonal migratory sika deer that used separate habitats seasonally, we defined summer period as a period the sika deer stay at the summer habitat and winter period as a period the sika deer remain at the winter habitat. And we analyzed the position data in summer and winter periods separately. We defined the position data on the way between winter and summer periods as migrating position data and the duration as migration periods.

We define the migration distance as the straight line distance between the centers of activity range between the periods of summer and winter. When there were more than one activity ranges formed within summer or winter period for same sika deer, we used the one formed at the beginning of the period for distance calculation.

To determine the characteristics of the seasonal habitat use of each individual, we analyzed the vegetation type of position data, snow depth, and land use regulation in different habitats. For vegetation type, we calculated the percentage of the number of points located in specific vegetation types within the home range of the each sika deer to show the vegetation use, and we collected vegetation data from a High-Resolution Land Use and Land Cover Map published by ALOS/ALOS-2 Science Project and Earth Observation Priority Research: Ecosystem Research Group of EORC (Earth Observation Research Center) and JAXA (Japan Aerospace Exploration Agency). To find the difference in snow depth between summer and winter habitats, we used the deepest record of average data surveyed in each GIS mesh created in 2012 and collected the data from the Digital National Land Information (Ministry of Land, Infrastructure, Transport and Tourism 2010). Further, to find the seasonal home range shift relative to the land use regulation, we calculated the overlap rate between home range and wildlife protection area. And we collected the range of wildlife protection area from the data of Digital National Land Information created in 2015 (Ministry of Land, Infrastructure, Transport and Tourism 2015).

11.5 Result

11.5.1 Monitored Individuals

We fit a total of 56 GPS collars to 37 sika deer (5 males and 32 females) in Oze area between May and December from 2013 to 2017 and 19 sika deer (6 males and 13 females) in Okuchichibu area between September and January from 2005 to 2006, 2009, and from 2015 to 2017 (Table 11.1).

Table 11.1 The sexual composition of collared sika deer in Oze and Okuchichibu areas of Kanto region, central Japan, from 2005 to 2017

Study area	Collared year	Male	Female	Total
Oze	2013–2017	5	32	37
Okuchichibu	2005–2017	6	13	19

Table 11.2 Movement pattern and sexual compositions of sika deer in Oze area, Kanto region, central Japan, from 2013 to 2017

Movement pattern	Movement type	Male	Female	Total	%
Seasonal migrant	Without stopover	2	15	17	45.9
	With stopover	3	8	11	29.7
Resident	–	–	1	1	2.7
Unknown	–	–	8	8	21.6
Total		5	32	37	100

11.5.2 Movement Patterns

We confirmed movement patterns of sedentary and migratory sika deer in both study areas. In Oze area, 28 out of 37 individuals were migratory (Table 11.2, Fig. 11.2). Only one sedentary sika deer was confirmed which was captured and collared in Nikko where the winter habitat of migratory deer is. The proportion of the sedentary and seasonal migratory sika deer accounted for 2.7% and 75.7%, respectively. We cannot define the movement pattern of the remaining eight individuals due to short tracking period.

Further, we classified the migratory sika deer into two types, i.e., migrant with or without stopover sites on the migration routes between summer and winter habitats. Eleven sika deer were seasonal migratory sika deer with temporal stopping sites on migration routes, and 17 were seasonal migratory sika deer without stopover site and migrated directly between summer and winter habitats. The seasonal migratory sika deer with stopover sites stayed for multiple days at each site during migration and showed variable patterns in duration and location of stay depending on individual and year. For example, ID1407 who migrated in spring 2015 from south to north stopped and stayed at five points temporarily on the migrating route to Oze marshlands (Fig. 11.3). ID1410 who migrated in autumn 2015 from north to south stopped and stayed longer at a point on the migrating route to winter habitat.

In Okuchichibu area, 10 out of 19 sika deer were migratory and 9 were sedentary (Table 11.3, Fig. 11.4). Seven out of ten migratory sika deer migrated seasonally between summer and winter habitats, and three migrated irregularly not depending on seasons. The proportion of the sedentary and seasonal migratory sika deer accounted for 47.4% and 36.8%, respectively. And the proportion of sedentary sika deer in Okuchichibu area was higher than that in Oze area (Tables 11.2 and 11.3).

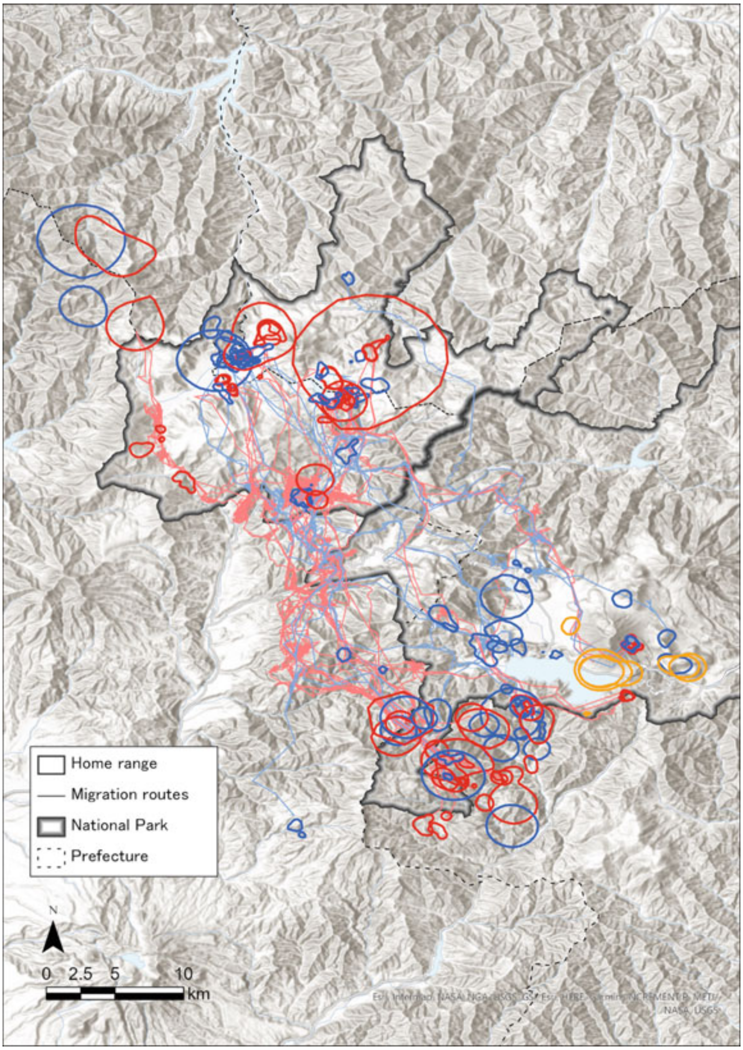


Fig. 11.2 Home ranges and migration routes of sika deer in Oze area (between Nikko and Oze marshlands), Kanto region, central Japan, from 2013 to 2017. Red indicates seasonal migratory sika deer using stopover sites, blue indicates sika deer not using stopover sites, and orange indicates sedentary sika deer

11.5.3 Migration Characteristics

The start of seasonal migration varied depending on the year and study areas. In Oze area, most migrations to summer habitats started from early April to mid-May for seasonal migratory sika deer and arrived from early May to early June (Table 11.4). On the other hand, for sika deer using stopover sites, the migration started from

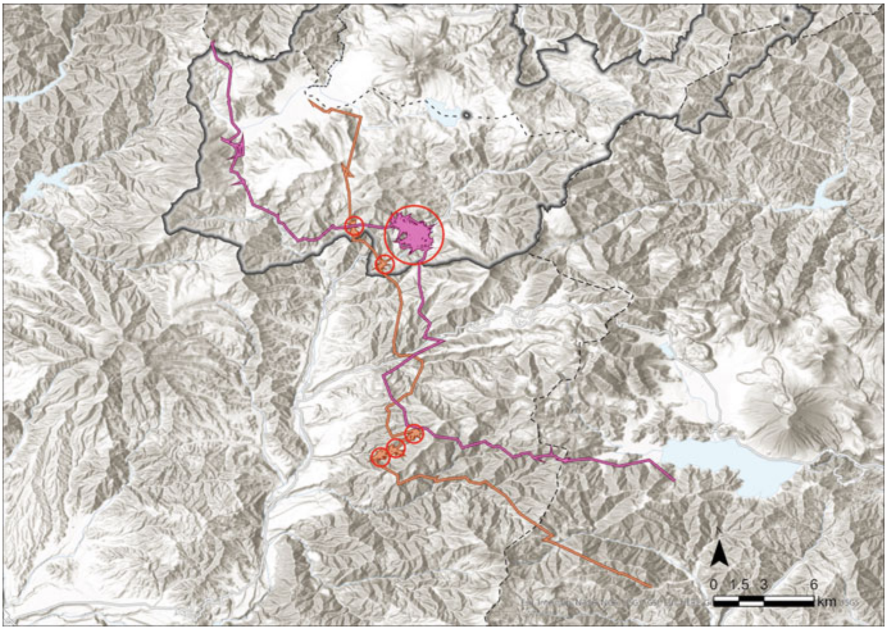


Fig. 11.3 Examples showing migration routes of sika deer using stopover sites in Oze area, Kanto region, central Japan. The brown line shows the spring migration route of ID1407, and the purple line shows the autumn migration route of ID1410. Red circles indicate stopover sites

Table 11.3 Movement patterns and sexual compositions of sika deer in Okuchichibu area, Kanto region, central Japan, from 2005 to 2017

Movement pattern	Male	Female	Total	%
Seasonal migrant	2	5	7	36.8
Irregular migrant	2	1	3	15.8
Resident	2	7	9	47.4
Total	6	13	19	100

mid-March to mid-April and arrived from early May to early June, showing a tendency of early start and synchronized arrival. When migrating to winter habitats, migratory sika deer who was not using stopover sites started migration from late October to late November and arrived from late October to early December. Sika deer who was using the stopover sites started migration from late September to early November and arrived from late November to early January, showing a late tendency to arrive their winter habitats. The average migration duration required for seasonal migratory sika deer without stopover site was 21.9 days, while it was about twice as long for individuals using stopover sites (41.0 days).

Sika deer in Okuchichibu area migrated to summer habitat starting from late March to mid-May and arrived from late March to late May, showing a 3–18-day duration, which was shorter in migration duration than that of sika deer in Oze area (Table 11.5). For migration to winter habitats, sika deer started in late November to early December and arrived from late November to early December, showing a

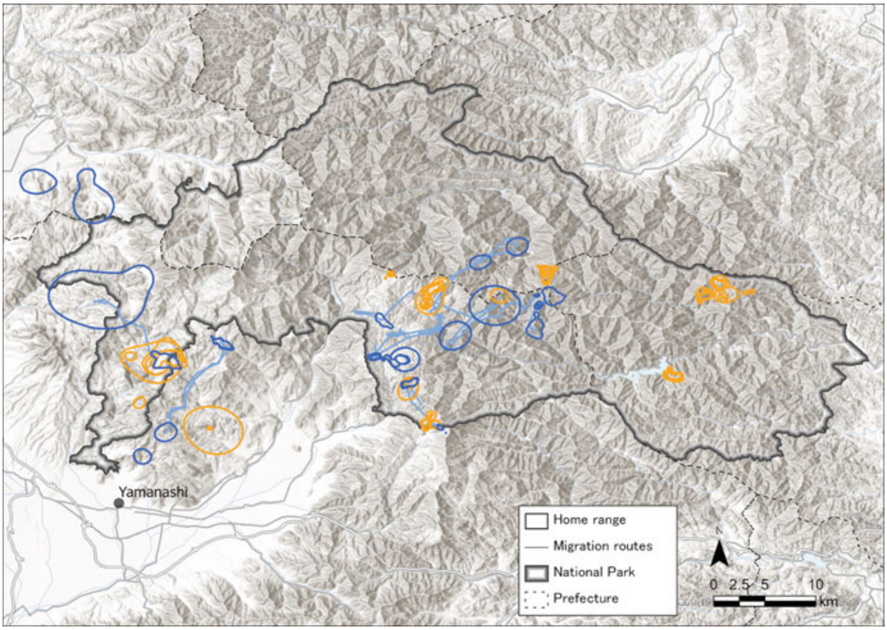


Fig. 11.4 Home ranges and migration routes of sika deer in Okuchichibu area, Kanto region, central Japan, from 2005 to 2017. Blue indicates migratory sika deer and orange indicates resident individuals

3–9-day duration, which was almost same as the opposite direction migration to summer habitat. However, we found one individual collared in 2016 migrated to the winter habitat in August and continually stayed in the winter area.

The migration distance in Oze area was 25.5 ± 7.6 (average ± SD) km for sika deer of seasonal migration without stopover and 30.6 ± 4.0 km for the deer with stopover, respectively (Fig. 11.5). The deer of seasonal migration with stopovers showed longer migration distances than the ones without stopover, and the longest migration distance reached 39.8 km. In Okuchichibu area, the average distance of migration was 8.1 ± 4.6 km which was much shorter than that in Oze area.

11.5.4 Home Range

In Oze area, the home range size of migratory sika deer was 4.4 ± 12.6 (average ± SD) km^2 in summer habitat, which was larger than that in winter habitat (3.6 ± 5.9 km^2, Table 11.6). The trend of seasonal difference of home range size in Okuchichibu area was same with that in Oze area and showed 6.7 ± 17.0 km^2 in summer habitat and 4.1 ± 7.2 km^2 in winter habitat.

Table 11.4 The difference in migration durations (day) between migratory sika deer with or without stopover sites during migration between summer and winter habitats in Oze area, Kanto region, central Japan

		Migrant without stopover				Migrant with stopover			
Year	Move direction to habitat	Departure date	Arrival date	Duration (day)	*n*	Departure date	Arrival date	Duration (day)	*n*
2013	Summer	–	–	–	–	–	–	–	–
	Winter	11/9–12/3	11/16–12/6	12	6	–	–	–	–
2014	Summer	3/2–4/28	5/30–6/5	38	2	–	–	–	–
	Winter	–	–	–	–	10/29–11/18	12/24–12/25	47	2
2015	Summer	5/17	6/6	20	1	3/10–4/8	5/17–6/26	73	3
	Winter	10/19–11/27	12/3–12/5	12	2	9/2–12/5	12/6–2016/1/29	57	8
2016	Summer	3/21–4/8	5/8	30	1	2/20–4/6	4/26–5/26	50	8
	Winter	7/30–11/6	10/10–11/15	9	3	10/25–12/9	11/17–2017/1/28	51	5
2017	Summer	–	–	–	–	4/13	5/13	30	1
	Winter	10/18–11/19	11/22–2018/1/1	32	5	9/26	11/26	61	1
Average of all sika deer				21.9				41.0	

Table 11.5 The difference in migration durations (day) between spring and autumn migration of migratory sika deer during migration between summer and winter habitats in Okuchichibu area, Kanto region, central Japan

Year	Move direction to habitat	Migration date and duration			
		Departure date	Arrival date	Duration (day)	*n*
2005	Summer	–	–	–	–
	Winter	10/22–12/5	10/29–11/14	9	3
2006	Summer	5/9	5/27	18	1
	Winter	12/1–12/3	12/3–12/6	3	2
2007	Summer	3/24	3/26–3/28	3	2
	Winter	–	–	–	–
2016	Summer	5/12–5/26	5/19–5/29	3	2
	Winter	8/11	8/15	4	1
Average				6.6	

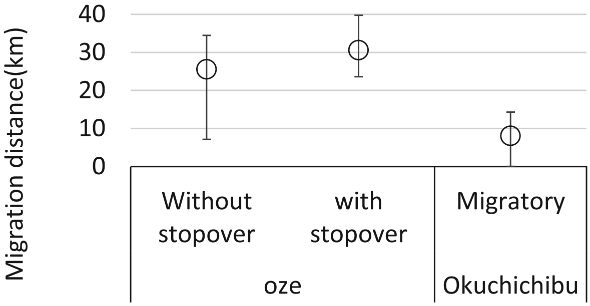


Fig. 11.5 Migration distance of seasonal migratory sika deer in both Oze and Okuchichibu areas, Kanto region, central Japan. Error bars mean standard deviation

Table 11.6 Home range size (km^2) of migratory sika deer in Oze and Okuchichibu areas, Kanto region, central Japan

Habitat	Oze area			Okuchichibu area		
	Mean	SD	*n*	Mean	SD	*n*
Summer	4.4	12.6	49	6.7	17.0	10
Winter	3.6	5.9	35	4.1	7.2	8

Table 11.7 Home range size (km^2) of sedentary sika deer in the areas of Oze and Okuchichibu areas, Kanto region, central Japan

Season	Oze area			Okuchichibu area		
	Mean	SD	*n*	Mean	SD	*n*
Spring	11.7	–	1	3.7	9.4	11
Summer	6.4	–	1	2.0	2.7	7
Autumn	–	–	1	1.1	1.2	12
Winter	7.6	–	1	1.8	2.3	12

On the other hand, the sedentary sika deer showed the largest home range in spring as 11.7 km^2 ($n = 1$) in Oze area and 3.7 ± 9.4 km^2 in Okuchichibu area, respectively (Table 11.7). The smallest seasonal home range was 6.4 km^2 ($n = 1$) in summer in Oze area and 1.1 ± 1.2 km^2 in autumn in Okuchichibu area, respectively.

Table 11.8 The overlap rate of home ranges of migratory sika deer for two consecutive years in Oze and Okuchichibu areas, Kanto region, central Japan

	Oze area		Okuchichibu area	
Habitat	Overlap rate (%)	*n*	Overlap rate (%)	*n*
Summer	90.7%	12	88.5%	3
Winter	94.8%	7	95.8%	1

The overlap rate of seasonal home ranges of migratory sika deer for two consecutive years was high. The lowest overlap rate also reached 88.5% in summer habitat in the Okuchichibu area (Table 11.8). The overlap rate in winter home range showed a higher value comparing with that in summer in both study areas, reaching 94.8% in Oze area and 95.8% in Okuchichibu area, respectively. We also found that sika deer tended to overwinter in almost exactly same area every year.

11.5.5 Habitat Use

11.5.5.1 Vegetation Use

In Oze area, the migratory sika deer used marshlands of Ozegahara and surrounding Lake Ozenuma as summer habitat and used forest environment in Nikko district including Ashio Mountains as winter habitat. Migratory sika deer used deciduous broad-leaved forest and deciduous conifer forest throughout years as well as grass cover (Fig. 11.6a). Sedentary sika deer used deciduous conifers mainly throughout tracking period and the utilization rate was higher than 80%. They also showed a relatively high use on deciduous broadleaved forest in early winter (December) and from late winter (February) to late spring (May) (Fig. 11.6b). In general, the migratory sika deer used deciduous broadleaved forest more than the sedentary sika deer throughout the year.

In Okuchichibu area, migratory sika deer used deciduous broad-leaved forest more, although the utilization rate was high in evergreen conifers from August to October (Fig. 11.7a). And that rate of broad-leaved deciduous forest showed an opposite trend with that of evergreen conifers. Sedentary deer used mainly evergreen coniferous and deciduous broad-leaved forests, and the utilization rate of evergreen coniferous forest was higher than that of deciduous broad-leaved forests. The utilization rate showed a constant trend throughout the years (Fig. 11.7b). Similar to that in Oze area, the migratory sika deer tented to use deciduous broad-leaved forest more than sedentary sika deer throughout the year.

11.5.5.2 The Use of Wildlife Protection Area

In Oze area, seasonal migratory sika deer had a higher overlap rate with wildlife protection area in both summer and winter habitats, but a lower overlap rate was

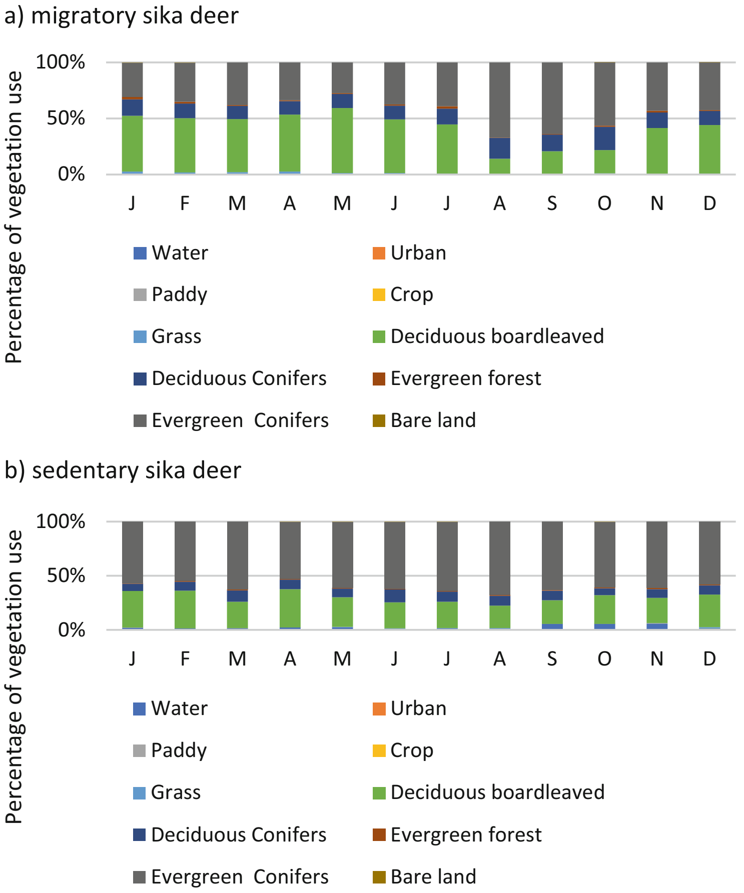


Fig. 11.6 Monthly vegetation use (% of vegetation type of the position points) of sika deer of different movement patterns in Oze area, Kanto region, central Japan (**a** migratory; **b** sedentary)

observed during the periods of seasonal migration from March to May and from October to November (Fig. 11.8a). For sedentary sika deer, most of home range was inside wildlife protection areas (Fig. 11.8b).

In Okuchichibu area, migratory sika deer had a relatively low overlap rate with wildlife protection area from April to August. Then that overlap rate accounted for about 10% from September to November and 20–50% from December to March, which showed much higher than that in other months (Fig. 11.9a). On the other hand, sedentary sika deer showed a higher overlap rate with wildlife protection area throughout the years comparing with that in migrants, ranging around 50–60% (Fig. 11.9b).

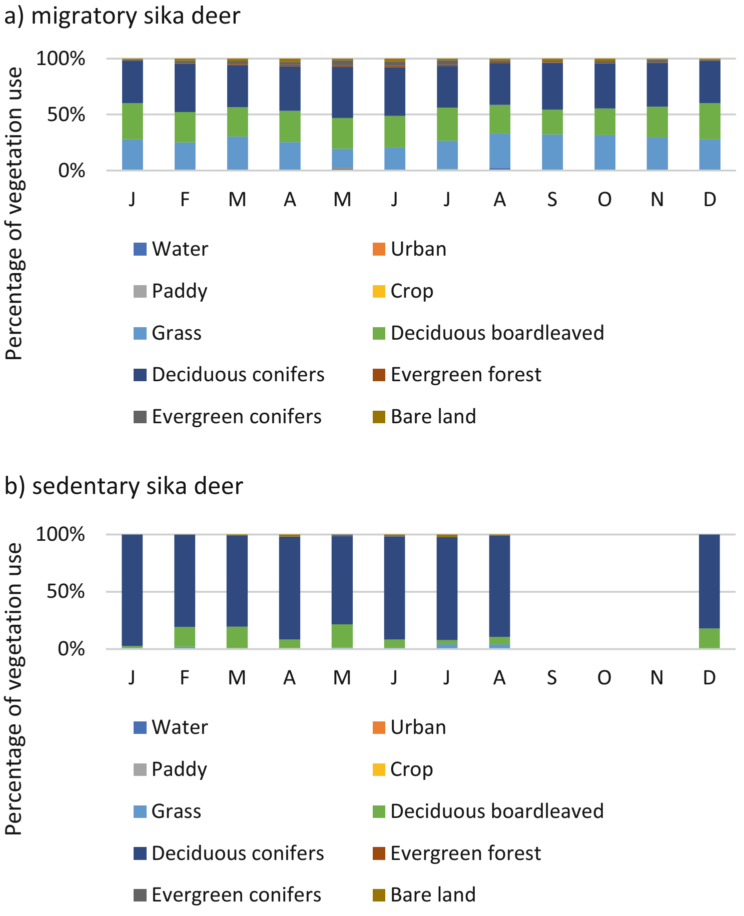


Fig. 11.7 Monthly vegetation use (% of vegetation type of the position points) of sika deer of different movement patterns in Okuchichibu area, Kanto region, central Japan (**a** migratory; **b** sedentary)

11.5.5.3 Snow Depth

Comparing the maximum snow depths in summer and winter habitats in Oze area, the snow depth of summer habitat in the marshlands of Oze district was 238 (IQR, 210–268) cm, while that of winter habitat in Nikko district was 53.1 (IQR, 47.3–56) cm, indicating a greater snow depth difference between summer and winter habitats (Fig. 11.10). In contrast to Oze area, the snow depth was 27 (IQR, 26–30) cm in summer habitat and was 28.9 (IQR, 28–30) cm in winter habitat in Okuchichibu area, respectively. Snow depth did not show obvious difference between summer and winter habitats like in Oze area (Fig. 11.11).

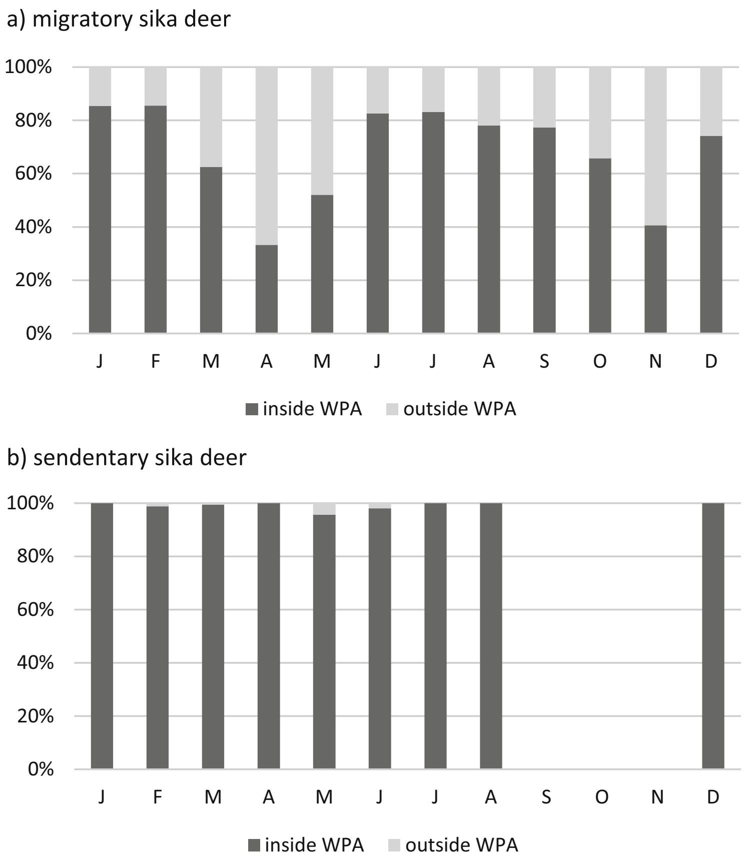


Fig. 11.8 The monthly overlap rate of home range with wildlife protection area (WPA) of sika deer of different movement patterns in Oze area, Kanto region, central Japan (**a** migratory; **b** sedentary)

According to the maximum snow depths of recent 30 normal years, the snow depth in Nikko district, the winter habitat of sika deer in Oze area, is close to the 50 cm limitation for sika deer moving freely (Fig. 11.12). In contrast to Oze area, the snow depth was less than 50 cm at most places in Okuchichibu area (Fig. 11.12).

11.6 Discussion

11.6.1 Characteristics of Migratory Distance

The mean seasonal migration distances in Oze area and Okuchichibu area were 25.5 and 8.1 km, respectively. The maximum migration distance of sika deer in Oze area

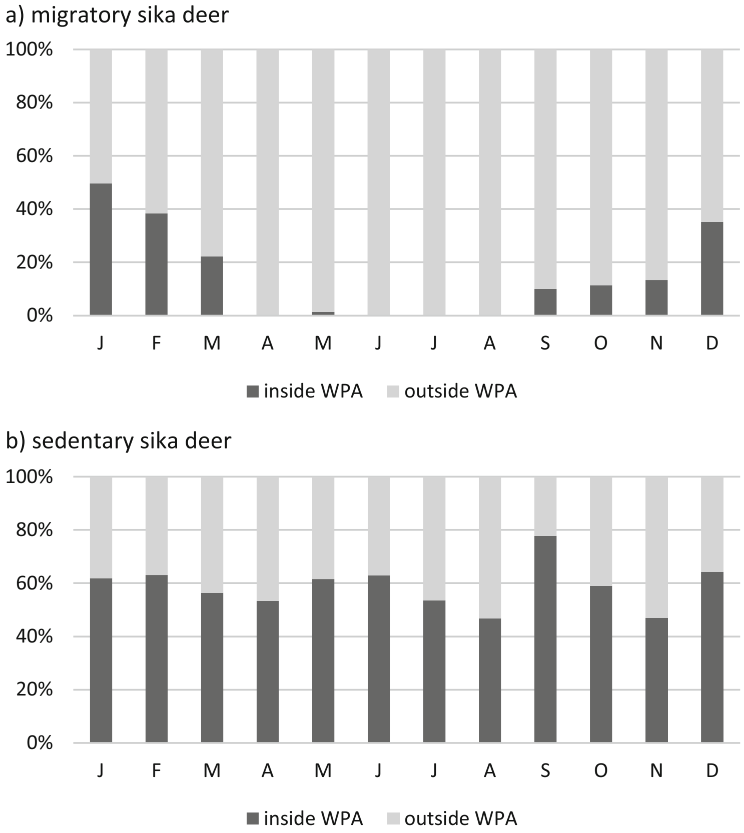
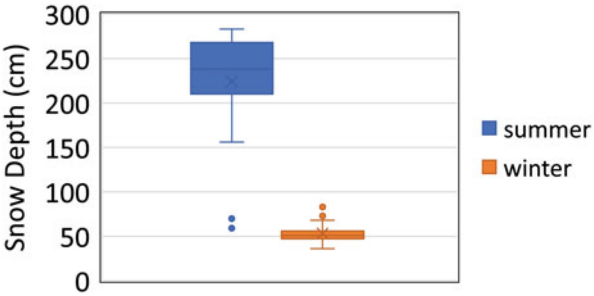


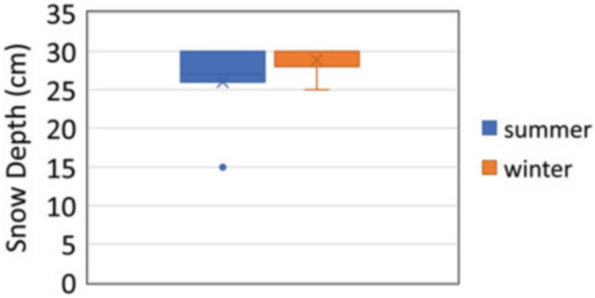
Fig. 11.9 The monthly overlap rate of home range with wildlife protection area (WPA) of sika deer of different movement patterns in Okuchichibu area, Kanto region, central Japan (**a** migratory; **b** sedentary)

Fig. 11.10 The snow depth difference between summer (Oze district) and winter (Nikko district) habitats in Oze area, Kanto region, central Japan. The box plots indicate the first quartile and median and third quartile, and (+) indicates the mean value



was 39.8 km. Seasonal migration distances of sika deer have been reported in Hokkaido, ranging from 7.2 to 101.7 km (Igota et al. 2004); in Kanto Mountains, ranging from 2.5 to 31.9 km (Takii et al. 2012a); and in Kirigamine Mountain ranging from 3.0 to 40.3 km (Takii et al. 2012b).

Fig. 11.11 The snow depth difference during winter between the home ranges of summer and winter habitats in Okuchichibu area, Kanto region, central Japan. The box plots indicate the first quartile and median and third quartile, and (+) indicates the mean value



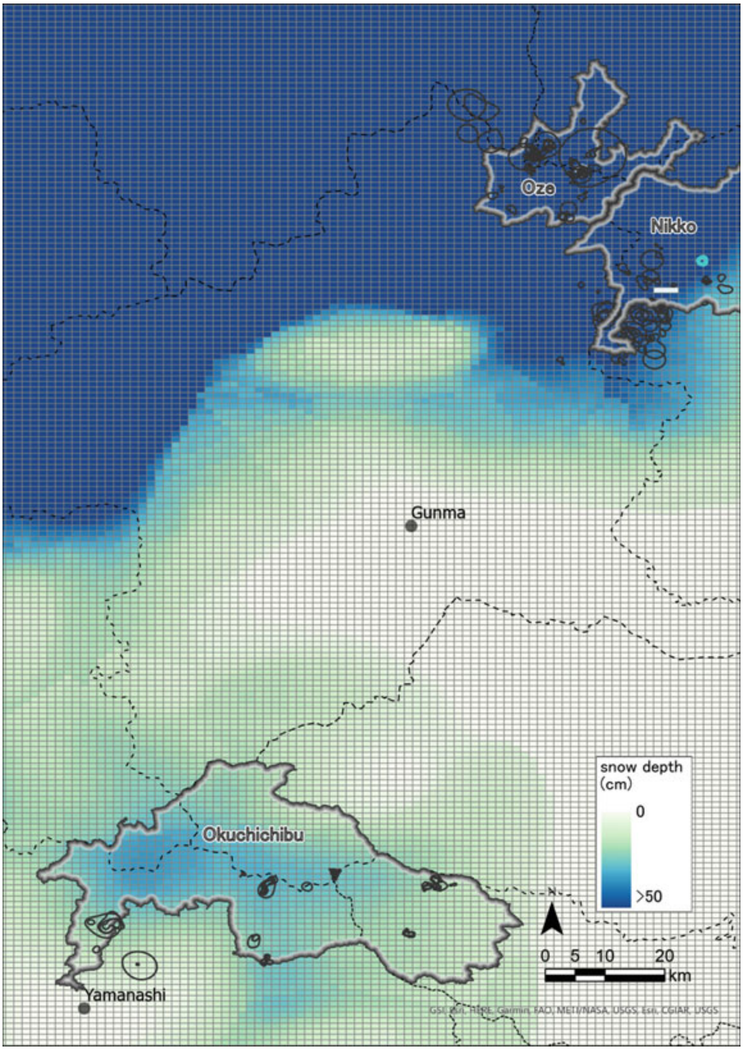


Fig. 11.12 Distribution of maximum average snow depth during the recent 30 years in the winter habitat in Oze and Okuchichibu areas, Kanto region, central Japan (gradient of blue indicates the variation of snow depth and dark blue the snow depth >50 cm)

11.6.2 Characteristics of Home Range

In both Oze and Okuchichibu areas, the size of the home range of seasonal migratory sika deer showed a tendency to be smaller in winter than in summer. The same trend has been reported in sika deer of Kanto Mountains (Takii et al. 2012a). The smaller winter home range is coincidence with the behavior for the ungulates in northern hemisphere to reduce food intake, activity, and movement within their limited home ranges during winter (Georgii 1980; Clutton-Brock and Harvey 1978; Georgii and Schröder 1983). In addition, the home range of migratory sika deer was larger than that of sedentary ones. Such a trend has also been reported for red deer (Kropil et al. 2015). In the case in Oze area, sika deer seems to take some time in forming stable home range after arriving at new habitat; the process may have resulted in a relatively larger home range for migratory sika deer. Further, migratory sika deer showed a high overlap rate in home ranges annually, especially in winter. The relatively higher overlap rate in winter may have resulted from the limited habitat available in winter due to heavy snow cover.

11.6.3 Factors of Seasonal Migration

In Oze area, 28 out of 29 and, in Okuchichibu area, 7 out of 19 were seasonal migratory sika deer. In terms of percentage, 96.6% in Oze area and 36.8% in Okuchichibu area were seasonal migratory sika deer and showed a higher proportion in Oze area than that in Okuchichibu area. The winter range of deer is determined not only by altitude but also by the distribution of snow depth in the habitat (Schmidt 1993; Takii et al. 2012a), and the determining factor for seasonal migration of deer is avoidance of deep snow cover that limits food abundance and daily movement in winter (Maruyama 1981; Uno and Kaji 2000; Igota et al. 2004). In particular, deer in Honshu of Japan have been reported to avoid areas where snow depth exceeds 50 cm (Maruyama 1981; Takatsuki 1992). The summer habitat of seasonal migratory sika deer in Oze area is located in marshlands of Oze district where the snow depth exceeds 2 m in winter. The heavy sown cover makes it difficult for sika deer to move as well as to obtain food. One sedentary deer in Oze area was collared in Nikko district, which is a part of the winter habitat of migratory sika deer in Oze area; this is why it can spend the winter without migrating. Therefore, deep snow cover was considered to be a main factor to drive seasonal migration in Oze area.

In contrast to deep snow in Oze area, the snow depth at summer habitat was about 30 cm in winter in Okuchichibu area, which was not significantly different from that at winter habitat. Therefore, it is unlikely that seasonal migration occurred for avoiding snow cover. The sedentary sika deer use about half of the home range in wildlife protection area throughout the year. On the other hand, seasonal migratory sika deer were mostly out of the protected area during summer, but the proportion using the protected area increased from December to March.

In Japan, the sports hunting starts from November 15 and finishes at February 15 of the following year (lasts until March 15 for deer and wild boar hunting in our study areas) outside wildlife protection areas. The higher overlap rate of home ranges with protected areas from December to March than that in other periods in Okuchichibu area may suggest that seasonal migratory sika deer tend to use protected areas as a refuge mainly in winter during the hunting season, for avoiding hunting risk. The seasonal change in using protected areas also suggests that the behavior of sika deer may change due to the effects of the hunting policy. Kamei (2010) and Takii et al. (2012a) reported the same trend for seasonal migration of sika deer in other areas.

In addition, deer harvest has been intensified due to the deer increase. Deer culling is conducted as permit hunting outside of the hunting period and is carried out both inside and outside of wildlife protection areas. The pressure of irregular deer culling in both timing and place may make the habitat use to become diversified and uncertain.

11.6.4 Characteristics of Migration with Stopover on Migrating Route

We confirmed two types of seasonal migration of sika deer in Oze area, i.e., seasonal migration with or without stopover sites on the migration route between summer and winter habitats. Both types had same summer and winter habitats, but the duration of the migration for the sika deer with stopover sites was longer than that of without stopover sites.

Seasonal migratory sika deer using stopover sites tended to arrive at their winter habitats later than those deer without stopover sites, although all of sika deer start migration at similar time to winter habitats. In contrast, in the case of migration to the summer habitat, they started migration about 1 month earlier than the individuals without stopover sites, but they arrived at summer habitat at same time. In other words, all migratory sika deer spent almost same duration in summer habitats, but the sika deer with stopover sites stayed shorter period in winter habitats than those deer without stopover sites.

Ashio Mountains of Nikko district is a winter habitat of the sika deer of Oze area, and the deer density became high for a long time before (Koganezawa et al. 2013). The high density of winter habitat will result in decrease in food resources and mass mortality during winter (Kaji et al. 1988, 2004; Takii 2013). The behavior for avoiding competition was confirmed when the density of deer becomes higher and higher in winter habitat (Mysterud et al. 2011). We considered that sika deer in Oze area may also avoid competition by shortening the period in winter habitat.

Sawyer and Kauffman (2011) reported that the quality of food at stopover sites on the way of seasonal migration was higher than that in winter habitat of mule deer. We hypothesize that sika deer using stopover sites in Oze area may also be for ingesting food efficiently by staying at stopover sites to shorten staying period in winter habitat where food is relatively scarce. In temperate areas, vertical migration from winter habitats in lower elevation to summer habitats in higher elevation is a common migration pattern (Mysterud et al. 2001), and migration allows large herbivores to have more continuous access to nutritious, newly emerged food (Fryxell and Sinclair 1988; Hebblewhite et al. 2008; Mysterud 2013). In other words, seasonal migration responds to changes in phenology and provides constant access to young, high-quality forages, which in turn influences the timing of seasonal migration (Mysterud et al. 2001). The possibility that migration using stopover sites occurs in accordance with the phenology transitions was considered. This is the first observation of sika deer using stopover sites during migration in Oze area in Japan, and the relationship between the use of stopover sites and the environmental conditions including food abundant and quality needs to be verified in the future.

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Chapter 12

Movement Patterns and Activity Range Characteristics of Sika Deer in the Tanzawa Mountains, Central Japan

Zhao-Wen Jiang, Takayuki Haneda, Koji Nagata, Yusaku Yamada, Koya Nagai, Naoki Machida, and Shunsuke Imai

Abstract To understand the characteristics of movement and activity range of sika deer (*Cervus nippon*), we tracked 42 individuals (33 females, 9 males) in the Tanzawa Mountains by GPS collars during 2008–2020. We confirmed 4 movement patterns as residential (27 deer, 64.3%), seasonal migration (12, 28.6%), mixed migration (1), and dispersal (2), showing a high residential proportion. Migration occurred in January–February, May, and October–November mainly. Seasonal migrants took 38 (12–190) hours and moved 6.2 (1.9–13.4) km with a 0–1200 m summer-winter elevation range. The annual core area and home range of all individuals were 1.106 and 4.117 km^2, showing a size order as disperser>seasonal migrants>mixed migrants>residents. The seasonal core area and home range of residents were 0.182 and 0.705 km^2, and that of adults in summer was the smallest. Core area and home range of seasonal migrants were 0.172 and 0.657 km^2, and most migrants showed a summer-low-winter-high type in elevation. The winter range of migrant males was smaller than that in summer resulting from narrow forage distribution and sever topography limiting the activity ranges. The concentrative

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Z.-W. Jiang (✉) · T. Haneda
Tokyo Division, Wildlife Management Office Inc., Hachioji, Japan
e-mail: jiang@wmo.co.jp; ta-haneda@wmo.co.jp

K. Nagata · K. Nagai
Division of Nature Conservation, Natural park and Wildlife, Kanagawa Prefecture Natural Environment Conservation Center, Atsugi, Japan
e-mail: nagata.d84q@pref.kanagawa.lg.jp; nagai.jk6y@pref.kanagawa.lg.jp

Y. Yamada
ROOTS Inc., Isumi, Japan
e-mail: yamada@roots-wl.com

N. Machida
Kensei Region Prefectural Administration Center, Kanagawa Prefecture, Kaisei, Japan
e-mail: machida.378@pref.kanagawa.lg.jp

S. Imai
Arid Land Research Center, Tottori University, Tottori City, Japan
e-mail: rainbow_f_t@yahoo.co.jp

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migration from hunting to protected areas around hunting start period suggests that hunting pressure might be an important migration trigger. The concentrative distribution of protected areas, high food availability due to snow decrease, and high overlap rate (80.8–86.2%) between activity range and protected area suggest that sika deer used summit areas as both refuge from hunting and feeding sites in winter.

12.1 Introduction

It has been revealed that sika deer (*Cervus nippon*) in the Tanzawa Mountains changed their distribution area from plains to mountain areas due to anthropogenic environmental modification (Yamane et al. 2007). Moreover, the deer density increased mainly in the wildlife protected areas at high altitudes, affecting the natural vegetation strongly (Yamane et al. 2007; Takeshita et al. 2016). The excessive feeding pressure by sika deer is not limited to barking damage of cedar (*Cryptomeria japonica*) and cypress (*Chamaecyparis obtusa*) in artificial forests, but also predicted to have a negative impact on natural forests, such as the decline of the understory vegetation (Tamura and Yamane 2017) and the death of trees due to barking and browsing, resulting in serious damage that inhibits forest regeneration (Tamura and Nakajima 2017). Furthermore, it is feared that this will lead to serious erosion (Wakahara et al. 2008; Chu et al. 2010) and a rapid decline in forest biodiversity in the future (Yamane et al. 2007).

For taking effective, efficient, and scientific measures for sika deer management, it is essential to understand the behavior and habitat use characteristics of the population. Movement pattern and activity range characteristic are the critical parts of animal behavior (Fryxell and Sinclair 1988; Harris et al. 2009 Mysterud et al. 2011). In order to understand the characteristics of movement and activity range of sika deer in the Tanzawa Mountains, we have conducted surveys by attaching Global Positioning System (GPS) collars to sika deer since 2008. It is expected that the behavioral characteristics of sika deer in the Tanzawa Mountains will be clarified through a comprehensive analysis of the accumulated GPS position data.

12.2 Study Area and GPS Collar Tracking

The Tanzawa Mountains is an inland mountainous area in northwestern Kanagawa Prefecture mainly and the connecting areas with Yamanashi and Shizuoka prefectures, located in the southwestern part of the Kanto region, central Japan. It stretches about 40 km from east to west and 20 km from north to south. The elevation ranges from 100 m to 1600 m, and the highest peak, Mt. Hirugatake, is 1673 m in elevation, and the terrain formed by ridges and valleys is complex. The southwest part of the mountain borders Yamanashi and Shizuoka prefectures and the ridge connects with Mt. Fuji (3776 m in elevation, the highest peak in Japan). The annual rainfall is about

2258 mm (Lake Tanzawa Weather Observatory). The mean monthly temperature is −2.4 °C–19.1 °C (Nabewari Weather Observatory) indicating a severe mountainous climate. Snow depth varies annually, and accumulated snow rarely gets deeper than a mean of 50 cm, except for the north slope in elevation over 1300 m (Yamane et al. 1997).

Almost all of the Tanzawa Mountains is covered with forest. Deciduous and evergreen broad-leaved forests are distributed on the steep terrain with thin topsoil of the peeled ground above 800 m in elevation (Yamane et al. 1997; Katsuyama 2012). The forests are dominated by beech (*Fagus crenata*) and oak (*Quercus crispula*), with Japanese hornbeam (*Carpinus japonica*) and Chonowski's hornbeam (*C. tschonoskii*). In limited areas on flat, stable ridges, there are camellia (*Camellia japonica*) and dogwood (*Cornus kousa*). There are also scattered larch (*Larix kaempferi*) plantations, but no subalpine vegetation exists (Katsuyama 2012). Artificial forests of cedar and cypress, mainly at the foot of the mountains (up to 1150 m in elevation), cover a vast area of about 47%, while natural forests of broad-leaved forests account for 53%. The area is home to a wide variety of creatures, including sika deer, black bear (*Ursus thibetanus*), Japanese serow (*Capricornis crispus*), wild boar (*Sus scrofa*), Japanese monkey (*Macaca fuscata*), raccoon dog (*Nyctereutes procyonoides*), red fox (*Vulpes vulpes japonica*), and other large- and medium-sized mammals. In the Tanzawa Mountains, for protecting the wildlife and ecosystem, wide ranges are designated as protected areas around summit and ridge in high elevation where sports hunting is prohibited. Outside the protected areas, sports hunting is allowed from November 15 to the end of February of the following year.

From 2008 to 2020, we have conducted tracking surveys for sika deer using GPS collars in the Tanzawa Mountains, including the areas of Central Tanzawa, Yadoriki, and the surrounding areas of Lake Miyagase, Mikuni Pass, the upper reaches of Nakagawa River, and Lake Tanzawa. The Central Tanzawa includes Mt. Tanzawa (1576 m in elevation), Mt. Hirugatake, Mt. Nabewari (1272 m in elevation), Mt. Tonodake (1491 m in elevation), and the surrounding areas. Yadoriki area is located in south, Lake Miyagase in northeast, Mikuni Pass in west, and Lake Tanzawa in southwest to the Central Tanzawa. The upper reach of Nakagawa River including Inukoeji Pass (1060 m in elevation), Mt. Omuro (1588 m in elevation), and the surrounding area is located in the northwest to the Central Tanzawa.

All of the sika deer were collared in the protested areas. We were able to track 42 individuals for more than 6 months, and the tracking period ranged from 190 to 729 days (Fig. 12.1, Table 12.1).

Of the 42 collared sika deer, 33 (78.6%) were females. Of the 33 females, 27 were adults. Among the juveniles, five were females and one male, while for the fawns were one female and one male (Table 12.2).

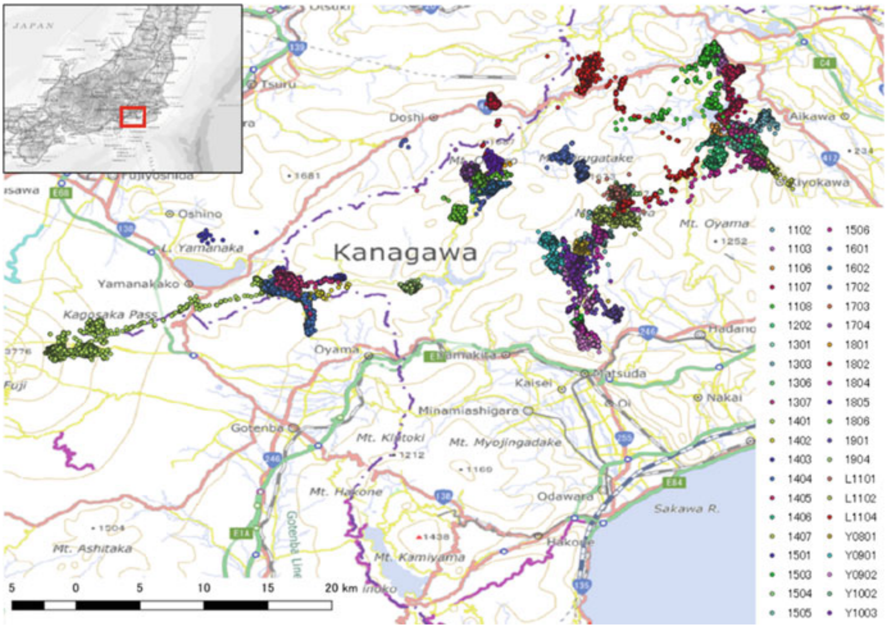


Fig. 12.1 The study area and the position data of all 42 sika deer with GPS collars in the Tanzawa Mountains, central Japan, from 2008 to 2020

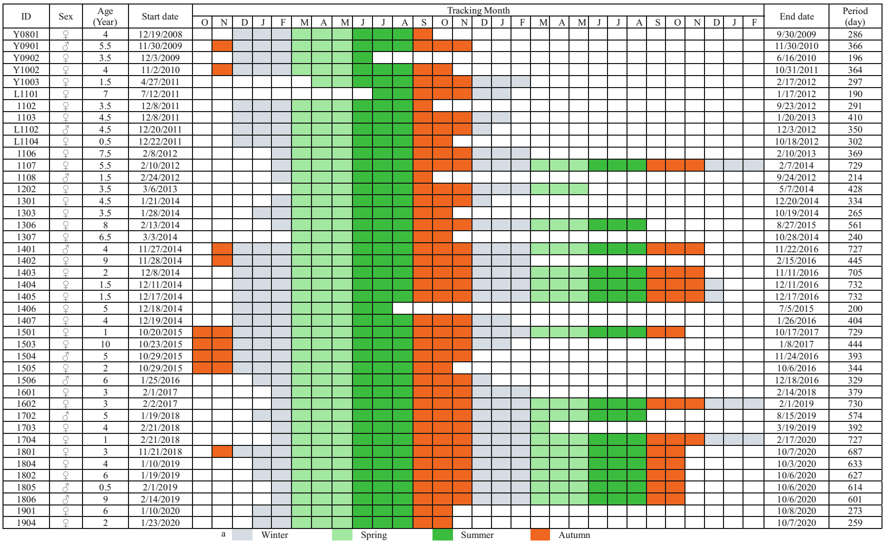
12.3 Methods

12.3.1 GPS Collars and Data Collection

We used five types of GPS collars, including Lotek 3300 from Lotek (Canada) in 2008, Tellus from Followit AB (Sweden) in 2009, GPS Plus and Vertex Plus from Vectronic (Germany) in 2011, and GLT-01 from Circuit Design (Japan) in some parts of 2012. The Vertex Plus GPS collar, used from 2013, has a satellite communication function that allows the collar to send data via Iridium satellite communication and the Internet. We applied for a program with 1 or 2 hours of positioning intervals that made the battery last for 1 to 2 years.

The data stored in the collar was acquired through a personal computer connected to the collars that were eventually recollected. If the collar could not be recollected, the data was acquired remotely using a dedicated communication device or via the Internet using the Iridium satellite.

Table 12.1 The basic information of the monitored sika deer using GPS collars and the data collect duration in the Tanzawa Mountains, central Japan, from 2008 to 2020[a]



ID	Sex	Age (Year)	Start date	Tracking Month																													End date	Period (day)
				O	N	D	J	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M	J	J	A	S	O	N	D	J	F		
Y0801	♀	4	12/19/2008			░	░	░	▒	▒	▒	🟩	🟩	🟩	🟧																		9/30/2009	286
Y0901	♂	5.5	11/30/2009		🟧	░	░	░	▒	▒	▒	🟩	🟩	🟩	🟧	🟧	🟧																11/30/2010	366
Y0902	♀	3.5	12/3/2009			░	░	░	▒	▒	▒	🟩																					6/16/2010	196
Y1002	♀	4	11/2/2010		🟧	░	░	░	▒	▒	▒	🟩	🟩	🟩	🟧	🟧																	10/31/2011	364
Y1003	♀	1.5	4/27/2011							▒	▒	🟩	🟩	🟩	🟧	🟧	🟧	░	░	░													2/17/2012	297
L1101	♀	7	7/12/2011										🟩	🟩	🟧	🟧	🟧	░	░														1/17/2012	190
1102	♀	3.5	12/8/2011			░	░	░	▒	▒	▒	🟩	🟩	🟩	🟧																		9/23/2012	291
1103	♀	4.5	12/8/2011			░	░	░	▒	▒	▒	🟩	🟩	🟩	🟧	🟧	🟧	░	░														1/20/2013	410
L1102	♂	4.5	12/20/2011			░	░	░	▒	▒	▒	🟩	🟩	🟩	🟧	🟧	🟧	░															12/3/2012	350
L1104	♀	0.5	12/22/2011			░	░	░	▒	▒	▒	🟩	🟩	🟩	🟧	🟧																	10/18/2012	302
1106	♀	7.5	2/8/2012					░	▒	▒	▒	🟩	🟩	🟩	🟧	🟧	🟧	░	░	░													2/10/2013	369
1107	♀	5.5	2/10/2012					░	▒	▒	▒	🟩	🟩	🟩	🟧	🟧	🟧	░	░	░	▒	▒	▒	🟩	🟩	🟩	🟧	🟧	🟧	░	░	░	2/7/2014	729
1108	♂	1.5	2/24/2012					░	▒	▒	▒	🟩	🟩	🟩	🟧																		9/24/2012	214
1202	♀	3.5	3/6/2013						▒	▒	▒	🟩	🟩	🟩	🟧	🟧	🟧	░	░	░	▒	▒	▒										5/7/2014	428
1301	♀	4.5	1/21/2014					░	▒	▒	▒	🟩	🟩	🟩	🟧	🟧	🟧	░															12/20/2014	334
1303	♀	3.5	1/28/2014				░	░	▒	▒	▒	🟩	🟩	🟩	🟧	🟧																	10/19/2014	265
1306	♀	8	2/13/2014					░	▒	▒	▒	🟩	🟩	🟩	🟧	🟧	🟧	░	░	░	▒	▒	▒	🟩	🟩	🟩							8/27/2015	561
1307	♀	6.5	3/3/2014						▒	▒	▒	🟩	🟩	🟩	🟧	🟧																	10/28/2014	240
1401	♂	4	11/27/2014		🟧	░	░	░	▒	▒	▒	🟩	🟩	🟩	🟧	🟧	🟧	░	░	░	▒	▒	▒	🟩	🟩	🟩	🟧	🟧	🟧				11/22/2016	727
1402	♀	9	11/28/2014		🟧	░	░	░	▒	▒	▒	🟩	🟩	🟩	🟧	🟧	🟧	░	░	░													2/15/2016	445
1403	♀	2	12/8/2014			░	░	░	▒	▒	▒	🟩	🟩	🟩	🟧	🟧	🟧	░	░	░	▒	▒	▒	🟩	🟩	🟩	🟧	🟧	🟧				11/11/2016	705
1404	♀	1.5	12/11/2014			░	░	░	▒	▒	▒	🟩	🟩	🟩	🟧	🟧	🟧	░	░	░	▒	▒	▒	🟩	🟩	🟩	🟧	🟧	🟧	░			12/11/2016	732
1405	♀	1.5	12/17/2014			░	░	░	▒	▒	▒	🟩	🟩	🟩	🟧	🟧	🟧	░	░	░	▒	▒	▒	🟩	🟩	🟩	🟧	🟧	🟧	░			12/17/2016	732
1406	♀	5	12/18/2014			░	░	░	▒	▒	▒	🟩	🟩																				7/5/2015	200
1407	♀	4	12/19/2014			░	░	░	▒	▒	▒	🟩	🟩	🟩	🟧	🟧	🟧	░	░														1/26/2016	404
1501	♀	1	10/20/2015	🟧	🟧	░	░	░	▒	▒	▒	🟩	🟩	🟩	🟧	🟧	🟧	░	░	░	▒	▒	▒	🟩	🟩	🟩	🟧	🟧					10/17/2017	729
1503	♀	10	10/23/2015	🟧	🟧	░	░	░	▒	▒	▒	🟩	🟩	🟩	🟧	🟧	🟧	░	░														1/8/2017	444
1504	♂	5	10/29/2015	🟧	🟧	░	░	░	▒	▒	▒	🟩	🟩	🟩	🟧	🟧	🟧																11/24/2016	393
1505	♀	2	10/29/2015	🟧	🟧	░	░	░	▒	▒	▒	🟩	🟩	🟩	🟧	🟧																	10/6/2016	344
1506	♂	6	1/25/2016				░	░	▒	▒	▒	🟩	🟩	🟩	🟧	🟧	🟧	░															12/18/2016	329
1601	♀	3	2/1/2017					░	▒	▒	▒	🟩	🟩	🟩	🟧	🟧	🟧	░	░	░													2/14/2018	379
1602	♀	3	2/2/2017					░	▒	▒	▒	🟩	🟩	🟩	🟧	🟧	🟧	░	░	░	▒	▒	▒	🟩	🟩	🟩	🟧	🟧	🟧	░	░	░	2/1/2019	730
1702	♂	5	1/19/2018				░	░	▒	▒	▒	🟩	🟩	🟩	🟧	🟧	🟧	░	░	░	▒	▒	▒	🟩	🟩	🟩							8/15/2019	574
1703	♀	4	2/21/2018					░	▒	▒	▒	🟩	🟩	🟩	🟧	🟧	🟧	░	░	░	▒												3/19/2019	392
1704	♀	1	2/21/2018					░	▒	▒	▒	🟩	🟩	🟩	🟧	🟧	🟧	░	░	░	▒	▒	▒	🟩	🟩	🟩	🟧	🟧	🟧	░	░	░	2/17/2020	727
1801	♀	3	11/21/2018		🟧	░	░	░	▒	▒	▒	🟩	🟩	🟩	🟧	🟧	🟧	░	░	░	▒	▒	▒	🟩	🟩	🟩	🟧	🟧					10/7/2020	687
1804	♀	4	1/10/2019				░	░	▒	▒	▒	🟩	🟩	🟩	🟧	🟧	🟧	░	░	░	▒	▒	▒	🟩	🟩	🟩	🟧	🟧					10/3/2020	633
1802	♀	6	1/19/2019				░	░	▒	▒	▒	🟩	🟩	🟩	🟧	🟧	🟧	░	░	░	▒	▒	▒	🟩	🟩	🟩	🟧	🟧					10/6/2020	627
1805	♂	0.5	2/1/2019					░	▒	▒	▒	🟩	🟩	🟩	🟧	🟧	🟧	░	░	░	▒	▒	▒	🟩	🟩	🟩	🟧	🟧					10/6/2020	614
1806	♂	9	2/14/2019					░	▒	▒	▒	🟩	🟩	🟩	🟧	🟧	🟧	░	░	░	▒	▒	▒	🟩	🟩	🟩	🟧	🟧					10/6/2020	601
1901	♀	6	1/10/2020				░	░	▒	▒	▒	🟩	🟩	🟩	🟧	🟧																	10/8/2020	273
1904	♀	2	1/23/2020				░	░	▒	▒	▒	🟩	🟩	🟩	🟧	🟧																	10/7/2020	259

[a] ░ Winter ▒ Spring 🟩 Summer 🟧 Autumn

Table 12.2 The sex and age structure of the collared sika deer in the Tanzawa Mountains, central Japan, from 2008 to 2020

Sex	Age class	No.	%	Age class (year)
Female	Fawn	1	2.4	<1
	Juvenile	5	11.9	1–2
	Adult	27	64.3	>2
Total ♀		**33**	**78.6**	
Male	Fawn	1	2.4	<1
	Juvenile	1	2.4	1–3
	Adult	7	16.7	>3
Total ♂		**9**	**21.4**	
Total		**42**	**100**	

12.3.2 *The Analyses of Position Data*

The data acquired from GPS collar include the information of longitude, latitude, and date/time of the sika deer's location. The attributes of position data from collars of different makers were converted and unified. For the analysis, we used position data of latitude and longitude of all individuals at 1- and 2-hour intervals.

12.3.2.1 Classification of Season and Year

By referring to the plant phenology in the study area, we defined the winter as December through February, spring as March through May, summer as June through August, and autumn as September through November. Since the winter season spans from 1 year to the next, we used the year of adjacent to January in the analysis and began in December. In order to make the most of the position data used, when analyzing the annual items with over 390 days of tracking, we defined the first year as the period from the start of tracking to the first 365 days and the second year as the period from the end of tracking to last 365 days.

12.3.2.2 Analyses of Position Data

We analyzed the movement patterns of sika deer during the tracking period, activity ranges (core area and home range), migration routes, and the relationship between activity ranges, migration destinations, and land use regulations (i.e., protected area or hunting area) using position data.

12.3.3 *The Confirmation of Movement Pattern*

Movement patterns of tracked individuals were typified from the pattern of temporal change over 1 year in net squared displacement (NSD), which is the square of the linear distance between an individual's position at one time and its position at each subsequent time (Bunnefeld et al. 2011).

For the analysis, each individual was divided into 1-year periods based on the start date of tracking, and the NSD was calculated using the position of the first tracking day as the starting point to analyze the movement pattern. Movement patterns were typified by the following five models (Bunnefeld et al. 2011).

The seasonal migration is a double sigmoidal model shown in Eq. (12.1), representing the return to the start area after 1 year.

$$\mathrm{NSD} = \frac{\delta}{1 + \exp\left(\frac{\theta s - t}{\varphi s}\right)} + \frac{-\delta}{1 + \exp\left(\frac{\theta a - t}{\varphi a}\right)} \tag{12.1}$$

Mixed migration is a double sigmoidal model shown in Eq. (12.2). Like the seasonal migration model, it has a migration period and a settlement period, but it does not return to the start place after 1 year.

$$\mathrm{NSD} = \frac{\delta s}{1 + \exp\left(\frac{\theta s - t}{\varphi s}\right)} + \frac{-\delta a}{1 + \exp\left(\frac{\theta a - t}{\varphi a}\right)} \tag{12.2}$$

The dispersal model is the sigmoidal model shown in Eq. (12.3), which moves and settles, but does not return to the start place after 1 year.

$$\mathrm{NSD} = \frac{\delta}{1 + \exp\left(\frac{\theta - t}{\varphi}\right)} \tag{12.3}$$

In Eqs. (12.1), (12.2), and (12.3), δ is the height of the graph (distance traveled), θ is the number of days (time) that the height of the graph reaches 1/2, φs is the number of days that the height of the graph goes from 1/2 to 3/4, φa is the number of days that the height of the graph goes from 1/2 to 1/4, and t is the number of days from the starting point. In Eq. (12.3), φ is the number of days until the height of the graph reaches 3/4.

The residential model is a linear model shown in Eq. (12.4), which does not move much. c represents a constant; NSD is unaffected by changes of time and remained a constant value.

$$\mathrm{NSD} \ = c \tag{12.4}$$

The nomadism pattern is a model with a linear line, as shown in Eq. (12.4). The individual will not settle and return to the start place after 1 year.

$$\mathrm{NSD} \ = \beta \times t \tag{12.5}$$

β is the slope of the line, and t is the number of days from the starting point. The distance from the starting point gradually increases.

12.3.4 Analyses of Activity Range

The fixed kernel method (Worton 1989) was used to calculate the activity range, with 90% defined as the home range (action range) and 50% as the core area (intensive use range). The AdehabitatHR package of the statistical software R (R Core Team 2017; Ver. 3.4.3) was used for the calculation. In the fixed kernel method, the spatial distribution density of the acquired position points greatly influences the results of the activity range calculation. Therefore, we do not calculate when the number of position points is less than 100 and the tracking period is less than half of the seasonal period.

12.3.4.1 Annual Activity Range

We calculated the annual activity range for all individuals. For individuals tracked less than 1 year, the core area and home range for the entire tracking period were used as annual values. Individuals that could be tracked for more than 390 days were analyzed on an annual basis.

12.3.4.2 Seasonal Variation of Activity Range in Residents

Because the movement patterns of nonresidential individuals are irregular and diverse, the timing and route of migration should have a large impact on the activity range. We limited the analysis for four seasonal variations of activity range in residential individuals only.

12.3.4.3 Activity Range of Migrant, Migrate Timing, and Moving Distance

There will be three movement patterns of migratory individuals: seasonal migrants, mixed migrants, and dispersers. Imaging the diversity of migration periods, we analyzed the activity range for winter and summer habitats of seasonal migrants but not for four seasons as in residential individuals. We classified the summer and winter habitat of the seasonal migrants, basing on the time series position data corresponding to the durations in winter and summer habitats. Moreover, the activity ranges were calculated for winter and summer habitats by excluding the position data during migration.

We used the position data during the migration period extracted from the position information from the point just before the start of the migration to the point after arrival at the destination of each individual to map the migration route in ArcGIS and decided the start and end timing of migration. The migration period was defined as the period between the position points just before the start of migration and just after arrival at the destination.

The distance traveled by sika deer was calculated from the parameters of the model of movement patterns: δ for seasonal migration and dispersal and δs and δa for mixed migration pattern.

12.3.5 The Relationship of Migration, Activity Range, and Protected Area

The timing, duration, and distance of migration and the percentage of area overlap between the activity range and the protected area were calculated. We hypothesize that plant phenology in spring and autumn should be related to the timing of migration. In addition, outside the protected areas, sports hunting can be done during the hunting period. We also hypothesize that the sika deer move to protected area around the start of hunting season for avoiding the hunting pressure. Information summary on migration routes, destination, and the timing of migration were used to examine affection on the migration and the change of activity range from hunting.

12.4 Results and Discussion

12.4.1 Movement Pattern

12.4.1.1 The Movement Pattern Confirmation

The distribution of position points for each individual was different, with some individuals concentrated in one area and others in two areas (Fig. 12.1). The 42 individuals were categorized into 4 movement patterns: seasonal migration ($n = 12$), mixed migration ($n = 1$), residential ($n = 27$), and dispersal ($n = 2$). No nomadism was identified (Figs. 12.2 and 12.3).

The NSD plots of the seasonally migratory individuals were of a one-peak (or one-valley) shape (Fig. 12.2). Residential individuals are fidelity to one area all year round, while seasonal migration individuals are attached to two areas (Figs. 12.1 and 12.2). Mixed migration deer are less attached to one area than seasonal migratory individuals (Figs. 12.1 and 12.3). The dispersal sika deer is characterized by the fact that it does not return to the original area after leaving the habitat site (Fig. 12.3).

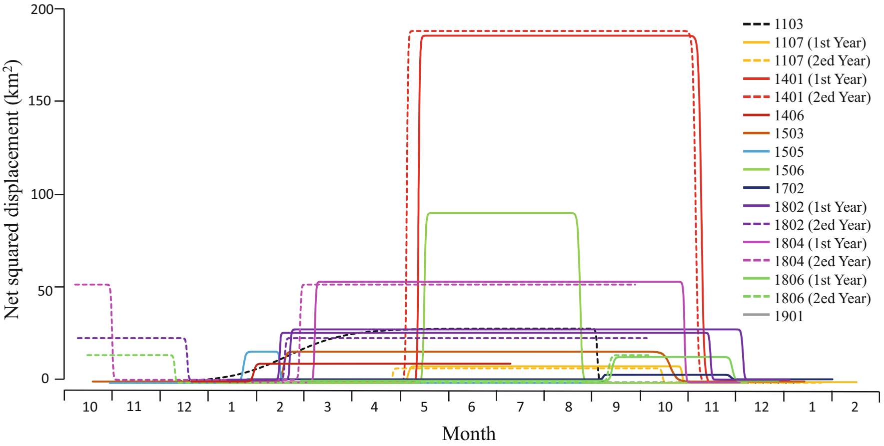


Fig. 12.2 The net squared displacement plots of 12 seasonal migration sika deer in the Tanzawa Mountains, central Japan

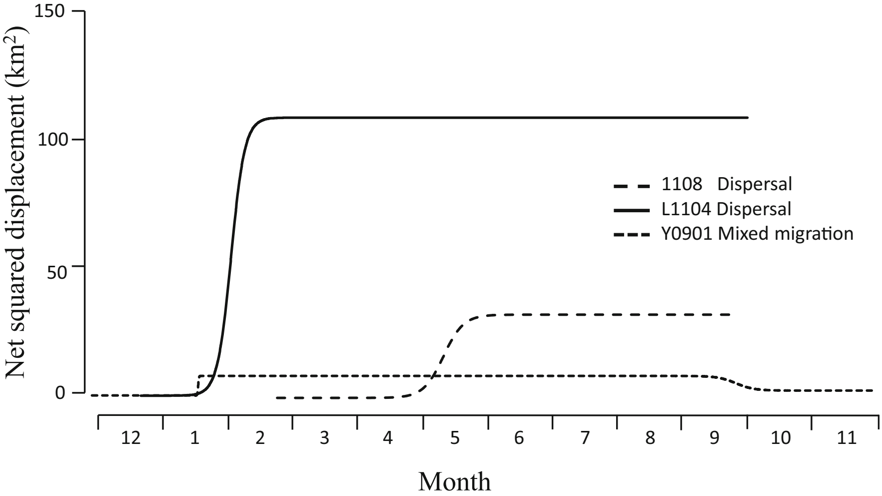


Fig. 12.3 The net squared displacement plots of the mixed migration and dispersal sika deer in the Tanzawa Mountains, central Japan

For the nine individuals that were tracked for 2 years, there was no yearly change in movement pattern (Fig. 12.2), with four individuals being residential and five being seasonal migrants.

12.4.1.2 The Characteristic of Movement Pattern in Age and Sex

Of the 42 individuals, 27 (64.3%) were residential, and 12 (28.6%) were seasonal migrants. Two dispersals and one mixed migrant both accounted for less than 5% of the total number of sika deer. One dispersal individual was a male juvenile, and the other was a female fawn. One individual of the mixed migration sika deer was an adult male (Table 12.3). The percentage of each sex in the movement pattern was 72.7% for residential females, higher than 33.3% for males. On the other hand, the proportion of seasonal migration in each sex is 24.2% females and 44.4% males (Table 12.3). The high proportion of residential individuals in the Tanzawa Mountains showed in this study is agreed with the results of Borkowwsk (1996) and Nagata (2005). The dispersal individual seems to be restricted to young females and males.

Partial migration is the coexistence of different movement patterns within the same species living in the same area (Chapman et al. 2011) and has been reported in red deer (*Cervus elaphus*) and moose in Europe (Ball et al. 2001; Cagnacci et al. 2011). The migration of sika deer in the Tanzawa Mountains is also a partial migration type (Table 12.3). The partial migration of sika deer was also reported in Nikko area, Tochigi Prefecture (Maruyama 1981); Hokkaido (Igota et al. 2004),

Table 12.3 The proportions of movement patterns in sex and age of sika deer in the Tanzawa Mountains[a], central Japan

	No. of sika deer										Proportion (%)								
	Female				Male						Female				Male				
	F	J	A	♀ Sum	F	J	A	♂ Sum	Total No.		F	J	A	♀ Sum	F	J	A	♂ Sum	Total (%)
Migration	–	–	8	8	–	–	4	4	12		–	–	19.0	24.2	–	–	9.5	44.4	28.6
Mixed migration	–	–	–	–	–	–	1	1	1		–	–	–	–	–	–	2.4	11.1	2.4
Residential	–	5	19	24	1	–	2	3	27		–	11.9	45.2	72.7	2.4	–	4.8	33.3	64.3
Dispersal	1	–	–	1	–	1	–	1	2		2.4	–	–	3.0	–	2.4	–	11.1	4.8
Total	1	5	27	33	1	1	7	9	42		2.4	11.9	64.3	100	2.4	2.4	16.7	100	100

[a] F, fawn; J, juvenile; A, adult; Sum, summary

the Northern Alps in central Japan (Takii et al. 2012a); and Mt. Goyo, in Iwate Prefecture (Takatsuki et al. 2000).

The movement pattern of sika deer may differ in age and sex. It has been suggested that migration in ungulates is not an instinctive behavior but a cultural behavior passed from individual to individual based on knowledge and memory (Fagan et al. 2013; Jesmer et al. 2018) by living in group. Since it takes time to memorize or learn the location of good food resources and migration routes, the seasonal migration form may be more common in individuals older than a certain age. We collared adult females mainly and the sample size was small for other age classes, so the age characteristics of seasonal migratory individuals could not be clarified. On the other hand, the dispersal pattern is seen when young individuals leave their parents, and the residential deer is thought to be a pattern that is not affected much by age. The results of this study were consistent that female fawn and juvenile males were easily to be dispersals.

The presence of seasonally migrating populations indicates the possibility of seasonal fluctuations in sika deer population density. In other words, there may be areas where population densities are higher during certain period. In the areas where the population density is high, there is concern about the impact on the vegetation due to feeding pressure by sika deer. It is also possible that these areas are suitable for efficient capture for population control.

12.4.2 The Characteristics of Seasonal Migrant Movements

12.4.2.1 Frequency of Migration and Moving Duration

We found that seasonal migrants migrated in all months except June and July, and migration frequency was low in summer (Fig. 12.4). The peak migration frequency of female sika deer was recorded in February and October, followed by January

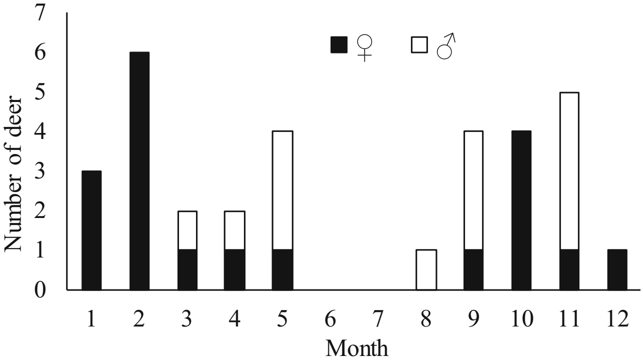


Fig. 12.4 The migrate timing and sexual difference of migratory sika deer in the Tanzawa Mountains, central Japan

Table 12.4 The migrating duration (hour) of seasonal migration sika deer in sex and season in the Tanzawa Mountains, central Japan

		Mean	SD[a]	Max	Min	n
Female	**Mean**	**42.7**	**41.5**	**190.0**	**12.0**	**18**
	Summer	**33.8**	19.4	68.0	14.0	10
	Winter	**53.8**	56.4	190.0	12.0	8
Male	**Mean**	**32.3**	**18.7**	**72.0**	**12.0**	**13**
	Summer	**30.3**	16.0	48.0	12.0	7
	Winter	**34.7**	21.2	72.0	12.0	6
Total		**38.3**	**34.3**	**190.0**	**12.0**	**31**

[a] *SD*: standard deviation

(Fig. 12.4). The higher frequency of male sika deer migration was recorded in May, September, and November (Fig. 12.4).

Seasonal migrants moved between summer and winter habitats and migrated from February to May and from September to November mainly, suggesting that seasonal changes in food resources relative to plant phenology may have affected the migration timing. It is conceivable that plant phenology may be a migratory factor in the spring migration of sika deer in the Tanzawa Mountains. It has been suggested that the timing of plant bud burst and migration may be linked in the spring migration of ungulates (Bischof et al. 2012; Merkle et al. 2016). This is because the young leaves of spring plants are a highly nutritious food resource that is easily digestible by ungulates. And the availability of high-quality food enhances the benefits of migration, which is referred to as the forage maturation hypothesis and has been shown to be true for spring migrations of multiple ungulate (Hebblewhite et al. 2008).

It is generally believed that the type of animal migration depends on the magnitude of spatial and temporal changes in food resources (Mueller and Fagan 2008), and seasonal migrations are those in which food resources vary seasonally and spatially and the variations are predictable to some extent. For example, red deer in the mountains of Switzerland are known to migrate seasonally, using higher altitude areas in summer and moving to lower altitude areas with less snow cover in winter (Zweifel-Schielly et al. 2009). Serengeti gnus (*Connochaetes gnou*) also migrate long distances seasonally in response to changes in vegetation during the rainy and dry seasons. Seasonal and predictable changes in the environment and spatial heterogeneity are expected to exist in the Tanzawa Mountains, and the environmental conditions for seasonal migration are expected to be favorable. The presence or absence of specific areas with high densities based on migration tracking and the evaluation of environmental conditions in such areas will be important themes for the population management.

Except for individual 1103 (Fig. 12.2), which had an extended migration period of 2146 hours (89.4 days) in spring, most of the seasonal migration individuals arrived at destination in short period after the start of migration, and did not move significantly thereafter. They remained to the same area for a certain period and repeatedly migrated between summer and winter habitats (Table 12.4, Fig. 12.2). The migration period of female sika deer was longer than that of males, and both males and females tended to spend more time moving to their winter habitat (autumn migration) than to their summer habitat (spring migration) (Table 12.4).

It has also been suggested that there are two types of migration strategies: surfer-type, which rides the wave of change in plant phenology, and jumper-type, which anticipates change and finish the migration shortly (Bischof et al. 2012; Merkle et al. 2016). The migration period of sika deer in this study ranged from 12 to 2146 hours, with a mean value of about 38 hours, suggesting that the migration period was too short for surfer-type and many individuals may have been jumper-type migrants. They were not surfers due to their memory of good food resources and migration routes, short migration distances, and the complexity of the ridge and valley topography, in addition to the possible effect from hunting activities.

12.4.2.2 Movement Distance and Elevation Variation

The maximum distance traveled by seasonal migrants was 13.4 km, the minimum was 1.9 km, and the mean was 6.2 km (Fig. 12.5, Table 12.5). For one case of mixed

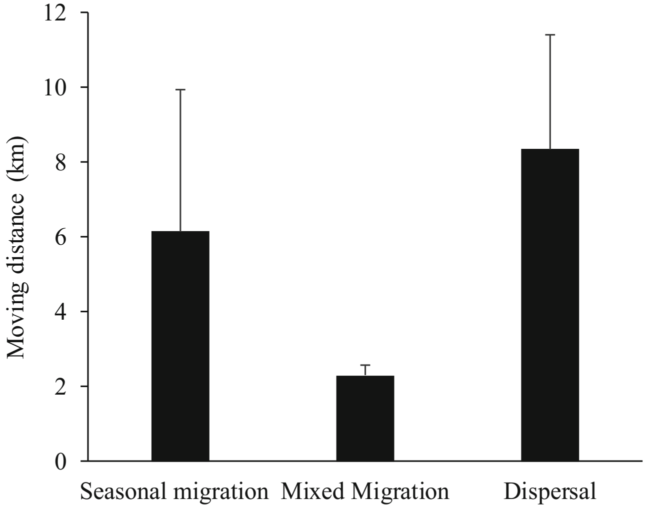


Fig. 12.5 The movement distances in different movement patterns of sika deer in the Tanzawa Mountains, central Japan

Table 12.5 The sexual differences in migration distance (km) of seasonal migration sika deer in the Tanzawa Mountains, central Japan

Sex	Mean	SD[a]	Min	Max	*n*
Female	4.7	1.7	2.2	7.6	19
Male	8.4	4.7	1.9	13.4	13
Total	6.2	3.7	1.9	13.4	32

[a] SD: standard deviation

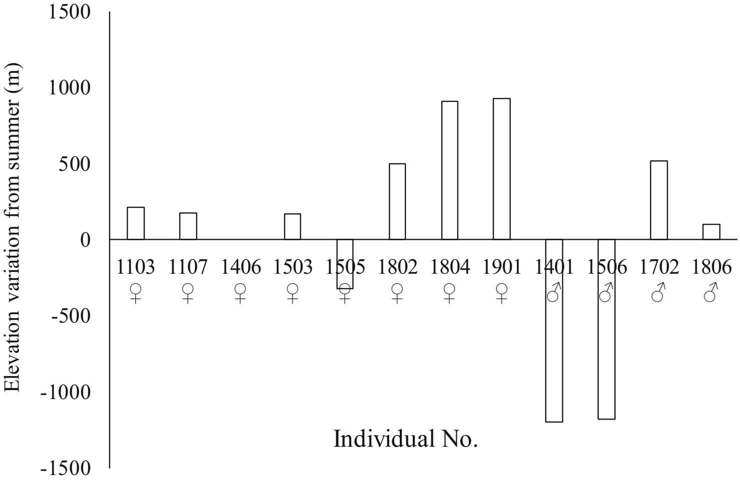


Fig. 12.6 The elevation variation in winter habitat comparing with those in summer of seasonal migration sika deer in the Tanzawa Mountains, central Japan

migration, the first migration was 2.5 km, and the second was 2.1 km (Fig. 12.5). The movement distances by two dispersals were 10.5 km and 6.2 km, with a mean of 8.35 km (Fig. 12.5).

The distance traveled by male individuals was longer than that of seasonally migrating females (Table 12.5). There was an approximately two times difference between the mean and maximum values and no sex difference in the minimum distance traveled.

More seasonal migrants (8 of 12 migrants, including 6 females and 2 males) used winter habitat with a higher elevation than that in the summer habitat (Fig. 12.6), and we named the seasonal movement-type as summer-low-winter-high (using low elevation areas in summer and autumn and high elevation ridgelines in winter).

For eight females, except for individual 1505 and 1406, six individuals used winter habitat at a higher elevation than that in summer. Individual 1505 collared near the top of Mt. Tanzawa temporarily moved to the southwest, about 4.0 km away, near Mt. Nabewari, and individual 1406 collared around Lake Miyagase moved to the opposite side of the lake without obvious elevation variation. Individual 1802 collared around Inukoeji Pass used mainly the ridges in winter and used summer habitat around 570 m in elevation. Individuals 1804 and 1901 collared around the Mt. Nabewari used the area around the summit in winter and used summer habitat at 300 m–370 m in elevation (Figs. 12.1, 12.6, and 12.7). The variation in elevation ranged from −320 m to 930 m for eight females (Fig. 12.6).

For four males, individual 1401 collared at the foot of eastern slope of Mt. Fuji at 1127 m in elevation in winter moved to west and used the eastern slope of Mt. Fuji up to around 2400 m in elevation in summer and autumn. Individual 1506 collared around Lake Miyagase at 250 m in elevation in winter moved to southwest and used Mt. Tanzawa summit area during summer. Individuals 1702 that collared at the

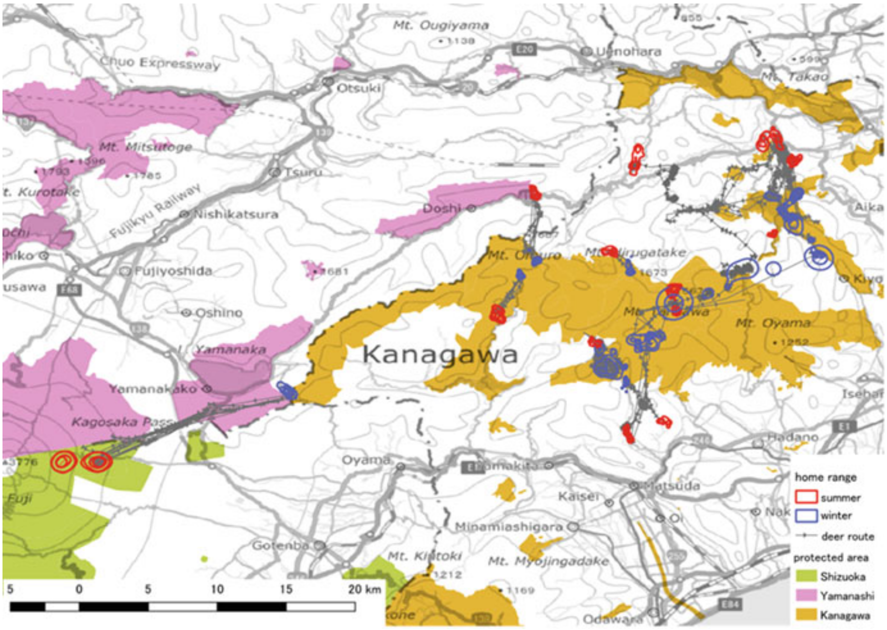


Fig. 12.7 The activity range of seasonal migration sika deer and the overlap degree with protected areas in Tanzawa Mountains, central Japan (15 deer including 12 seasonal migration, 1 mixed migration, and 2 dispersal)

Mt. Hirugatake used the area around the summit in winter and used an area about 1100 m in elevation in autumn. Individual 1806 collared at about 750 m in elevation in winter used an area about 650 m in elevation in autumn (Figs. 12.1, 12.6, and 12.7). The variation in elevation ranged from −1200 m to 520 m for all four male deer (Fig. 12.6).

The seasonal movement of summer-low-winter-high was also observed in the Chichibu Mountains and was suggested a reaction influenced by hunting (Takii et al. 2012b) and Shiranuka Hills in eastern Hokkaido (Igota et al. 2004). The ridge was mainly covered with snow during winter in the past in the Tanzawa Mountains. However, in recent years, mild winter has resulted in less snow cover (Yamane et al. 2007) even in the higher elevations with global warming. Therefore, it is thought that food resources such as dwarf bamboo grasses are more abundant on the ridge than in lower elevation areas and that sika deer could use the ridge even in winter when there was little snow (Yamane et al. 2007; Murakami et al. 2007; Katsuyama 2012).

There is information that the lower vegetation in the study area was thick with dwarf bamboo more than 50 years ago (Yamane et al. 1997; Konohira 2007; Yamane et al. 2007), even in the lower elevation areas. However, the dwarf bamboo is only found on the ridges in high elevation (Murakami et al. 2007; Yamane et al. 2007; Katsuyama 2012), which suggests that sika deer may have eaten up the dwarf bamboo and understory vegetation in the low area mainly. Looking at the time axis of sika deer distribution and density change, after food resources become scarce in lower areas where sika deer have inhabited at high densities for a long time, they are likely to migrate for searching new food resources, changing movement patterns, and dispersing. Sika deer migration to lower elevations between mid-February and early March is thought to be due to their search for nutritious and easily digestible shoots in early spring at lower elevations. It is still essential to confirm whether the changes in the environment condition, especially the snowfall, affect movement patterns annually.

Besides the relative abundant food resources around the summit and ridge in high elevation during winter, the concentrative distribution of protected areas should be another factor for sika deer to use the habitats in high elevation as refuges during hunting season in winter. The peak migration frequencies in November and February were coincident with the start and end of the hunting season also supporting the influence on migration timing from hunting.

The high percentage of sika deer with a summer-low-winter-high movement type suggests that efficiently capture in the lower elevation areas during the summer-autumn would be helpful to control the density of sika deer in the high elevation areas in winter. In order to take efficient measures for managing sika deer efficiently, the movement characteristics should be focus on by taking into account the snow condition annually. In addition, if more individuals use the higher areas during the winter, it is predicted that adverse effects on the fragile vegetation on the ridge lines will be more likely to occur, and it is necessary to take appropriate vegetation protection measures as soon as possible.

In the central area of the Tanzawa Mountains, around Mikuni Pass which are adjacent to Mt. Fuji, the elevation difference between the winter and summer habitats was great, and the migration distance was also longer comparing with other areas. A characteristic of migration in both north and south directions (Fig. 12.7) was observed in the boundary ridges of Inukoeji Pass between Yamanashi and Kanagawa prefectures, together with the multiple moving directions in other areas suggesting that the direction of migration was not constant and regular in the area of Tanzawa Mountains.

12.4.2.3 Migration Timing, Destination, and Land Use Regulations

Seasonal migration sika deer migrated between hunting areas and protected areas or between protected areas. However, we did not find the migration within hunting areas (Fig. 12.7). Although all seasonal migration sika deer were collared inside protected areas, during summer or autumn they moved to other protected areas or hunting areas (Fig. 12.7).

Sports hunting start from November 15 and finish at the end of February outside protected areas. For examining the effect of hunting performance on migration timing, we summarized moving direction and timing of total 14 migrations around hunting start periods (1 month before and after the hunting start) of 12 seasonal migrants. We found that 8 of 14 migrations, accounting for 57.1%, occurred from

Table 12.6 Proportion of movement number within 1 month before and after the hunting start to total movement between protected and hunting areas in the Tanzawa Mountains, central Japan

Move direction when hunting start	Before and after 1 month		Other period		Total Move no.
	Move no.	Proportion (%)	Move no.	Proportion (%)	
From hunting to protected area	7	87.5	1	12.5	8
Between protected areas	3	50.0	3	50.0	6
Total move and proportion	10	71.4	4	28.6	14

hunting to protected areas, and the proportion was higher than that migrating between protected areas (Table 12.6). We also found that 10 of 14 migrations, accounting for 71.4%, occurred around the hunting start periods, and the proportion was higher than that in other period (Table 12.6, Fig. 12.7).

We confirmed seven migrations around hunting start period, accounting for 87.5% of the total eight moves from hunting to protection areas (Table 12.6). The proportion of migration from hunting area to protected areas around hunting start was obviously higher than that of other period. The higher proportion of leaving hunting areas to protected areas of winter habitat suggests a concentrate period of leaving hunting areas and hunting should be one of the important factors triggering sika deer migration for avoiding hunting pressure.

12.4.3 Activity Range and Protected Area

12.4.3.1 Annual Activity Range and Protected Area

Residential sika deer attached to a single small area, while seasonally migratory individuals used a small area, similar to residential individuals, except for short periods of migration (Fig. 12.8). The sites used by the residential and seasonally migratory sika deer did not change from year to year, indicating a solid fidelity to the sites where they used.

The mean annual core area and home range of all sika deer were 1.106 and 4.117 km^2, respectively. The size of the core area and home range became smaller in the order of dispersal, seasonal migratory, mixed migratory, and residential individuals (Table 12.7, Fig. 12.9). The difference between the largest (migrant males) and smallest (residential females) core area and home range of adult sika deer was 33.3 and 29.2 times, respectively.

The difference between the maximum (adult males) and minimum (fawn male) annual core area and home range of residential sika deer was 4.2 and 3.2 times, respectively. From the distribution of annual core area and home range of all individuals, it was confirmed that the core area and home range overlapped each other in same region. It was also confirmed that the core area and home range of

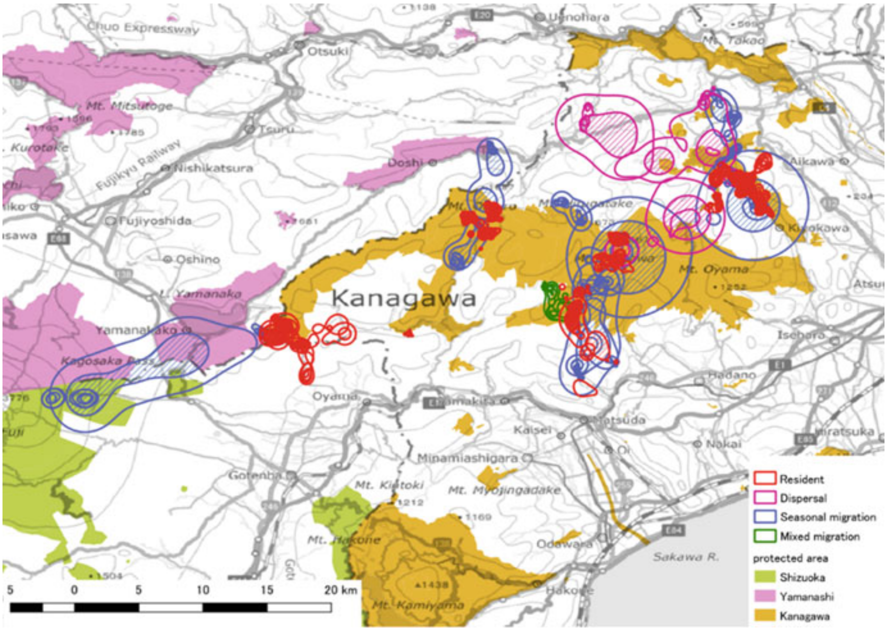


Fig. 12.8 The annual activity range of sika deer and the overlap degree with protected areas in the Tanzawa Mountains, central Japan

seasonal migration sika deer formed in two areas and resident individuals formed in only one area with overlapping core area and home ranges.

Both core area and home range of each sex in the seasonal migration pattern were larger in males than in females. The difference in core area and home range were 5.1 and 4.8 times larger than that of females, respectively.

The annual core area and home range of each sex in the residential sika deer were larger for adult males than for adult females, as in the seasonal migration pattern. The difference in core area and home range were 1.7 and 1.5 times, respectively, and the difference was smaller than that in seasonal migration pattern.

Comparing the annual core area and home range of males and females in each age group in residential sika deer, both core area and home range of females were smaller in adults than in juveniles. However, males increased with age in the order from fawn, juvenile, to adult in both core area and home range (Table 12.7).

The core area and home range of all sika deer overlapped with some or all of the protected area, accounting for more than 70% of the total area (Table 12.8). The relative high overlap of annual activity range with protected area should be resulted from that sika deer were collared inside the protected areas, the fidelity to certain habitat, and the preference on protected area as a refuge during hunting season in the Tanzawa Mountains.

Table 12.7 The annual activity range (km^2) of all sika deer in sex, age, and movement pattern in the Tanzawa Mountains[a], central Japan

		Core area(km^2)						Home range(km^2)								
		Mean			*SD*			Mean			*SD*			*n*		
Movement pattern	Sex	F	J	A	F	J	A	F	J	A	F	J	A	F	J	A
Migration	Mean	–	–	2.914	–	–	4.986	–	–	10.334	–	–	16.690	–	–	20
	Female	–	–	1.204	–	–	0.857	–	–	4.440	–	–	2.931	–	–	13
	Male	–	–	6.091	–	–	7.357	–	–	21.281	–	–	24.404	–	–	7
Mixed migration	Male	–	–	0.469	–	–	–	–	–	2.656	–	–	–	–	–	1
Residential	Mean	0.074	0.203	0.194	–	0.121	0.164	0.340	0.829	0.759	–	0.651	0.740	1	6	36
	Female	–	0.225	0.183	–	0.122	0.165	–	0.902	0.729	–	0.690	0.753	–	5	33
	Male	0.074	0.095	0.311	–	–	0.097	0.340	0.461	1.089	–	–	0.459	1	1	3
Dispersal	Mean	2.710	3.268	–	–	–	–	14.069	15.662	–	–	–	–	1	1	–
	Female	2.710	–	–	–	–	–	14.069	–	–	–	–	–	1	–	–
	Male	–	3.268	–	–	–	–	–	15.662	–	–	–	–	–	1	–
Total		1.392	0.641	1.153	1.318	1.079	3.227	7.204	2.948	4.152	6.864	5.226	10.900	2	7	57

[a] F, fawn; J, juvenile; A, adult

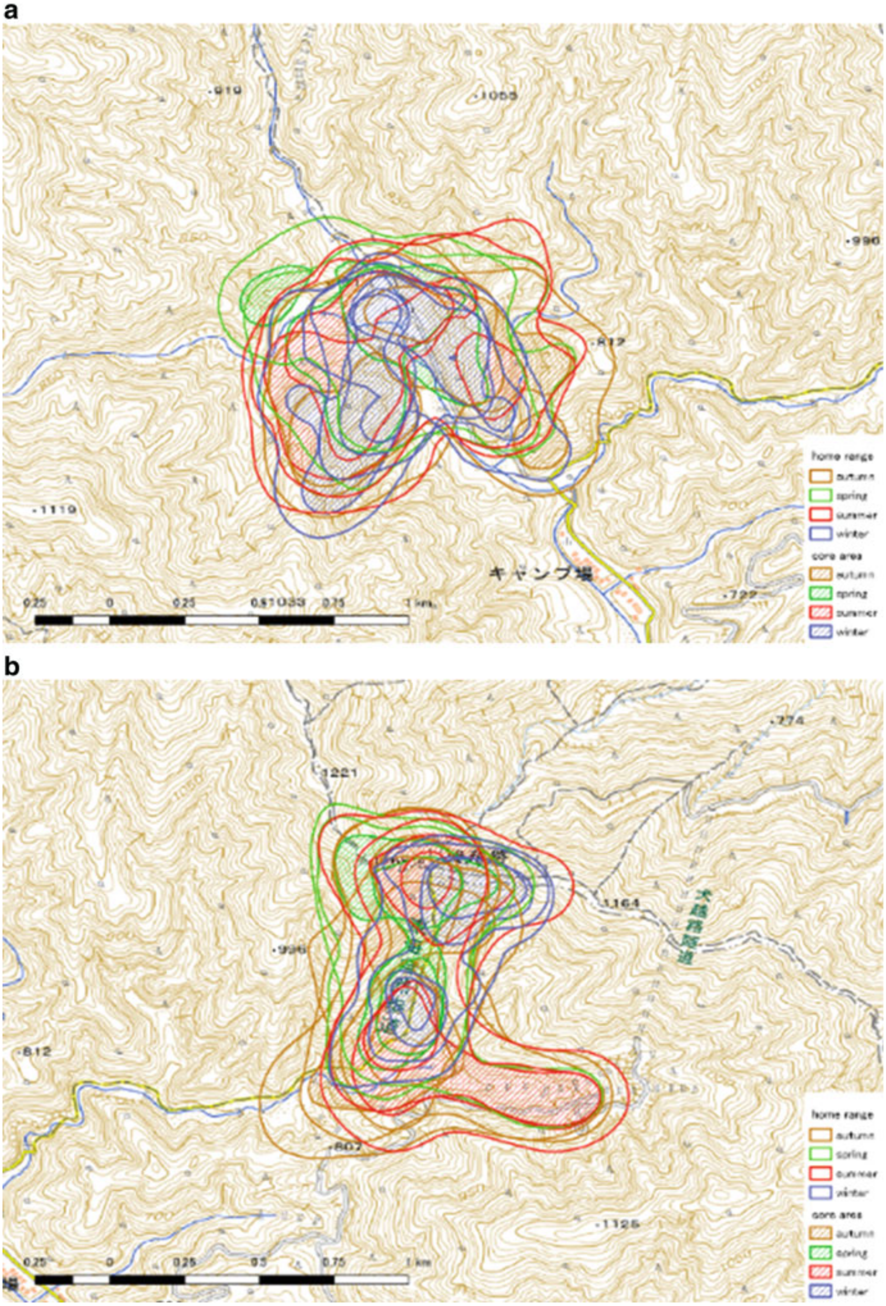


Fig. 12.9 The examples of the seasonal activity ranges of 2 years to show the fidelity of the residential sika deer to small ranges in the Tanzawa Mountains, central Japan, ID 1704 (a) and ID 1801 (b)

Table 12.8 The overlap rate (%) between annual activity ranges and protected areas of sika deer in the Tanzawa Mountains[a], central Japan

	Core area	Home range
Mean	**72.4**	**71.2**
SD	34.4	29.4
Min	0.0	5.6
Max	100	100
n	71	71

[a] *SD*: standard deviation

12.4.3.2 Seasonal Activity Range of Residential Sika Deer and Protected Area

The seasonal mean area of core area and home range of residential sika deer were 0.182 and 0.705 km^2, respectively. We did not confirm an identical seasonal trend in the size of core area and home range for all sex and age groups. However, the largest core area showed in spring of adult females and winter of adult males. And the largest home range showed in winter of adult and juvenile females and in autumn of adult males and spring of juvenile males. We also found that the core area and home range of adult sika deer were the smallest in summer comparing with other seasons (Table 12.9). The smallest summer activity range in adult sika deer might be resulted from the most abundant food environment in summer comparing with other seasons. Sika deer could obtain enough food to meet their digestive physiological need within a small area if the food is abundant. The mean area of all core areas and home range was less than 0.5 and 1.8 km^2, respectively, showing a narrow trend (Table 12.9, Fig. 12.7, 12.9).

The core area and home range of each sex of residential adult sika deer tended to be larger in males than in females. The difference in core area and home range was about 1.7 and 1.5 times larger than that of females, respectively.

The core area and home range of female sika deer tended to decrease with age, while the male sika deer tended to increase with age (Table 12.9). The same tendency as that of the annual core area and home range was also observed, and these sex differences in the change in the size of core area and home range with age may be attributed to the formation of different behavioral characteristics with growth. Both female and male sika deer are thought to move with their parents for about 6 months after birth. As juveniles, the activity range becomes wider than that of fawns due to their separation from their parents. As females become adults, they use a fixed area, and their activity range is thought to become smaller. As males become adults, they tend to expand their range in order to secure their own territory.

All of the residential individuals overlapped some or all of the protected area, and together with the core area and home range, they occupied around 80% of the protected area (Table 12.10). Similar to the annual activity range, the high overlap rate between the activity range and the protected area of residential sika deer should be resulted from that sika deer were collared inside the protected areas and the stronger fidelity to certain habitat of the residents mainly. The increased overlap rate between the activity range and protected area of residential sika deer comparing with

Table 12.9 The activity ranges (km^2) of residential sika deer in season, sex, and age in the Tanzawa Mountains[a], central Japan

		Core area (km^2)						Home range (km^2)						*n*		
		Mean			*SD*			Mean			*SD*					
Sex	Season	F	J	A	F	J	A	F	J	A	F	J	A	F	J	A
Female	**Sum♀**	**–**	**0.320**	**0.173**	**–**	**0.285**	**0.186**	**–**	**1.535**	**0.652**	**–**	**1.577**	**0.808**	**–**	**7**	**110**
	Winter	–	0.394	0.185	–	0.270	0.221	–	2.047	0.785	–	1.749	1.089	–	3	25
	Spring	–	0.265	0.208	–	0.285	0.282	–	1.151	0.782	–	1.309	1.127	–	4	28
	Summer	–	–	0.129	–	–	0.059	–	–	0.466	–	–	0.232	–	–	31
	Autumn	–	–	0.175	–	–	0.078	–	–	0.607	–	–	0.335	–	–	26
Male	**Sum♂**	**0.080**	**0.078**	**0.291**	**–**	**0.032**	**0.173**	**0.304**	**0.293**	**1.006**	**–**	**0.109**	**0.597**	**1**	**5**	**7**
	Winter	–	0.035	0.406	–	–	0.261	–	0.166	1.266	–	–	0.799	–	1	2
	Spring	0.080	0.108	0.266	–	–	0.008	0.304	0.418	0.931	–	–	0.058	1	1	2
	Summer	–	0.070	0.155	–	0.028	0.022	–	0.256	0.473	–	0.097	0.055	–	2	2
	Autumn	–	0.104	0.386	–	0.000	0.000	–	0.368	1.705	–	–	–	–	1	1

[a] F, fawn; J, juvenile; A, adult; SD, standard deviation

Table 12.10 The overlap rate (%) between activity ranges and protected areas of residential sika deer in the Tanzawa Mountains[a], central Japan

	Winter		Spring		Summer		Autumn	
	Core area	Home range	Core area	Home range	Core area	Home range	Core area	Home range
Mean	**85.1**	**82.0**	**79.7**	**80.5**	**86.0**	**86.5**	**87.3**	**87.5**
SD	31.0	27.9	34.1	28.3	31.3	25.7	28.5	24.0
Min	0.0	1.4	0.0	9.1	0.0	4.7	0.0	13.8
Max	100	100	100	100	100	100	100	100
n	46	45	38	37	36	35	38	37

[a]*SD*: standard deviation

Table 12.11 The activity ranges (km^2) of seasonal migrants in season and sex[a] in the Tanzawa Mountains, central Japan

		Core area (km^2)		Home range (km^2)		*n*
Sex	Season	Mean	*SD*	Mean	*SD*	
Female	**Mean**	**0.116**	**0.121**	**0.429**	**0.393**	**22**
	Summer	0.104	0.047	0.369	0.147	12
	Winter	0.131	0.170	0.502	0.551	10
Male	**Mean**	**0.266**	**0.319**	**1.043**	**1.215**	**13**
	Summer	0.462	0.385	1.643	1.431	5
	Winter	0.143	0.185	0.668	0.869	8
Total		**0.172**	**0.229**	**0.657**	**0.857**	**35**

[a]*SD*: standard deviation

that in the annual activity range suggests that residential sika deer are using the protected area more intensively than the sika deer with other movement patterns.

12.4.3.3 Activity Range of Seasonal Migrants and Protected Area

The characteristic of the core area and the home range of the seasonal migrants was the formation of two areas, the activity ranges of summer and winter habitats (Fig. 12.7). The mean area of core area and home range were 0.172 and 0.657 km^2, respectively, showing a narrow trend (Table 12.11, Fig. 12.7). Excluding the migration period, the size of the core area and home range in winter and summer habitats of the seasonal migrants were almost same as that of the residential sika deer. These results suggest that the activity areas of seasonal migration sika deer are similar to those of the residents after excluding the migration route.

The core area and home range of each sex in seasonal migrants were larger in males than in females. The sexual differences in core area and home range were 2.3 and 2.4 times larger in males than females, respectively (Table 12.11). However, the sexual differences were absent in both core area and home range in winter habitat, whereas the activity range of the summer habitat was larger in males than in females,

Table 12.12 The overlap rate (%) between activity ranges and protected areas of seasonal migration sika deer in Tanzawa Mountains[a], central Japan

	Winter		Summer	
	Core area	Home range	Core area	Home range
Mean	**86.2**	**80.8**	**37.3**	**36.3**
SD	28.8	27.9	44.4	43.3
Min	0.0	12.5	0.0	0.0
Max	100	100	100	100
n	27	27	23	23

[a] *SD*: standard deviation

with a 4.4 and 4.5 times difference in core area and home range, respectively. The activity range in summer habitat also was larger in males than in both sexes in winter.

The expansion of the summer range in male sika deer was also observed in the Chichibu Mountains (Takii et al. 2012b). In high elevation areas, the narrower distribution of abundant understory plants that provide food for sika deer on mountain peaks and ridgelines and the severer topography than that in summer habitat might limit the activity and resulted in a small winter range (Takii et al. 2012b). And longer stay period in summer habitat in low elevations than in winter habitat should also contribute to the larger activity ranges in summer.

All seasonal migration sika deer overlapped some or all of the protected areas, and together with their core areas and home ranges, they occupied less than 40% of the protected areas in summer and more than 80% in winter (Table 12.12). The lower overlap rate with the protected area in summer than that in winter suggests that seasonal migrants use a larger area during the physical recovery period (Table 12.11) to secure food in summer period and habitat. In addition, most sika deer migrated in February and September–November, and they will stay in summer habitat for about 7 to 8 months from March to October. The longer period should contribute to the wider activity range also than that in winter habitat. Meanwhile, the high proportion of overlap rate with protected areas during winter suggests that hunting may drive sika deer to use protected area as refuges from hunting pressure during the hunting season in winter.

12.4.4 Triggers for the Start of Seasonal Migration

Factors that influence sika deer migration include natural factors, such as seasonal changes of food resources, temperature, precipitation, and snow cover relative to topography, physiological factors such as reproductive activity (Loe et al. 2005; Jesmer et al. 2018), and human factors such as hunting pressure (Holdo et al. 2010; Mysterud et al. 2011; Lone et al. 2015). We consider the snow depth, matting activity, seasonal variation of food distribution, and hunting pressure to influence the migration timing. However, it seems challenging to determine a single indicator corresponding to the migration trigger of sika deer in the Tanzawa Mountains according to the research results.

12.4.4.1 The Depth of Snow Cover

The start of five migrations of female deer during January–February from higher winter habitat to summer habitat in low elevation (Figs. 12.4 and 12.6) in the Central Tanzawa area and the upper reaches of the Nakagawa River area might be influenced by the increase of snow cover. However, we have no records for the depth of snow cover in detail around the migration periods and the home range, which we cannot discuss in detail.

Snow depth more than 50 cm has a strong influence on sika deer behavior (Takatsuki 1992). As a common sense, deer migrate to lower elevations and overwinter for avoiding the harsh alpine environment in winter, especially deep snow (Nicholson et al. 1997; Igota et al. 2004; D'Eon and Serrouya 2005). In general, there are few places where the snow cover exceeds 50 cm even at high elevations in the Tanzawa Mountains; meanwhile, the terrain is steeper and deer could use the southern slopes with less snow in winter (Yamane et al. 2007). The use of high elevation area in winter shown by the higher proportion (66.7%) of summer-low-winter-high type suggests that the snow depth should not be a constant trigger for starting migration in the Tanzawa Mountains.

Considering the variations in migration timing and opposite moving directions, it seems no consistent trend as meteorological stimulators, such as changes in temperature and precipitation, to drive deer migration in the Tanzawa Mountains.

12.4.4.2 Matting Activity Due to Physiological Cycle

The physiological cycle of the breeding might be a trigger of the migration of some adult males. Individual 1702 and 1806 migrated from winter habitat to summer habitat in early to mid-September when the mating season starts and returned to winter habitats in late November or early December when the mating period ended (Figs. 12.4 and 12.6). The migration timing from winter to summer habitat differs from that of the other adult males from March to May, and the migrations were most likely a breeding migration for securing the matting partners resulting from the reproductive physiological cycle inside body, rather than external factors.

Characteristic movements may occur depending on sex and age during the mating season in autumn and the calving season in spring (Bischof et al. 2012). The fidelity of females to their home range is stronger than that of males (Cagnacci et al. 2011). Comparing with females, it is more possible that some adult males move around the mating season to secure harems in the Tanzawa Mountains.

12.4.4.3 Variation of Food Resource and Hunting Pressure

One of the benefits from seasonal migration should be the access to high nutritious or abundant food resource. The migrations to winter habitat in higher elevation summits and ridge areas around the Mt. Hirugatake, Mt. Nabewari, and Inukoeji Pass from late October to December and to summer habitat in lower areas from February to May can be considered to be the result of demanding for relative abundant and nutritious food resources.

Since the high concentration of protected areas on the ridges at high elevations in the Tanzawa Mountains, it is possible that sika deer used the area as a refuge from hunting. The relative high availability of food plants, such as dwarf bamboo grasses, due to the decreasing snow cover meets the demand on food of sika deer in winter. The records of seasonal migration entering protected areas of sika deer during hunting season in Tanzawa Mountains (Kanagawa Prefecture and Wildlife Management Office 2003) also support that deer migrate seasonally to avoid hunting pressure. The same migration type was also observed in the Chichibu Mountains (Takii et al. 2012b). Red deer have also been reported to use high altitude, harsh terrain environments in winter (Pepin et al. 2008).

The higher proportion of migration from hunting to protected areas around the period of hunting start suggests that deer tend to leave the hunting area and move to protected areas for avoiding hunting pressure. Furthermore, the higher overlap rate of activity ranges with protected areas in winter than that in summer suggests that deer tend to use protected areas mainly in hunting season, the period covering winter, for avoiding hunting risk. Therefore, comparing with other factors, the hunting pressure might be the most possible trigger that drives sika deer start migration to winter habitat. In addition, the behavior of start migration before hunting in some sika deer may be inherited from parents or learned from other deer in group due to hunting which has been conducted continually by same annual schedule.

It is likely that great migration timing variation besides around hunting start period may have been resulted from the nuisance kill pressure. Since nuisance kill has been conducted irregularly in protected areas, the migration timing has become diversified widely.

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Chapter 13
Movement Patterns of Sika Deer Around Mt. Fuji, Central Japan

Takahiro Ohba

Abstract The behavioral pattern of sika deer (*Cervus nippon*) inhabiting the areas around Mt. Fuji was analyzed based on the results of tracking 11 animals wearing GPS collars. In this area, the home range size of the sika deer was calculated based on long-term tracking data (compiled over 6 months), and it was found to be 147.5 ± 59.9 ha (mean ± SD, $n = 4$) and 259.6 ± 127.5 ha ($n = 3$) for females and males, respectively. Mt. Fuji has a topography that exhibits elevation differences of more than 2000 m from the alpine zones to the hilly areas. Moreover, since it is an independent peak located toward the Pacific Ocean, it has relatively little snow cover; however, the amount and duration of snow cover depend on the rate of snowmelt, which, in turn, varies with the direction and elevation of the location. Ten of the eleven individuals were seasonal migrants; five moved along the contour lines, while six had a vertical home range shift that was orthogonal to the contour line. It may be suggested that the radial erosion troughs, which have been formed in this area, might restrict the behavior of sika deer, thereby forming a longitudinal behavioral zone.

13.1 Introduction

Mt. Fuji (peak: 35.36 °N, 138.73 °E) is Japan's highest active volcano (3776 m above sea level). It is located about 100 km west of central Tokyo, straddling the boundaries of Shizuoka Prefecture to the south and Yamanashi Prefecture to the north. It is an independent peak near the Pacific coast, and its southern foot reaches the sea (Suruga Bay). Mt. Fuji is recognized globally as a symbol of Japan for its beautiful mountain scenery, and in 2013, a part of the mountain range was included in the UNESCO's World Heritage List as "Mt. Fuji: Object of Faith and Source of Art."

T. Ohba (✉)
Forestry and Forest Products Research Center, Shizuoka Prefectural Research, Institute of Agriculture and Forestry, Hamamatsu, Shizuoka, Japan
e-mail: takahiro1_ohba@pref.shizuoka.lg.jp

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The high density of deer population around Mt. Fuji, both in Yamanashi (Iijima et al. 2013) and Shizuoka prefectures (Shizuoka Prefecture 2019), has affected the vegetation of the region (Takeuchi et al. 2011; Nagaike 2020). Based on the Wildlife and Hunting Act of 2012, a Specified Wildlife Conservation and Management Plan (for sika deer) was developed in the Fuji area (Mishima City, Susono City, Gotemba City, Fuji City, Fujinomiya City, Numazu City, and some areas in Sunto County) including Mt. Fuji of Shizuoka Prefecture. Over the years, there has been an increasing pressure to reduce/control the population of the sika deer.

The purpose of this study was to determine the seasonal migration pattern, home range, and intensively used habitat of the sika deer so that a population management plan can be formulated based on the observed behavioral characteristics, with particular emphasis on improved efficiency of capture.

13.2 Study Area

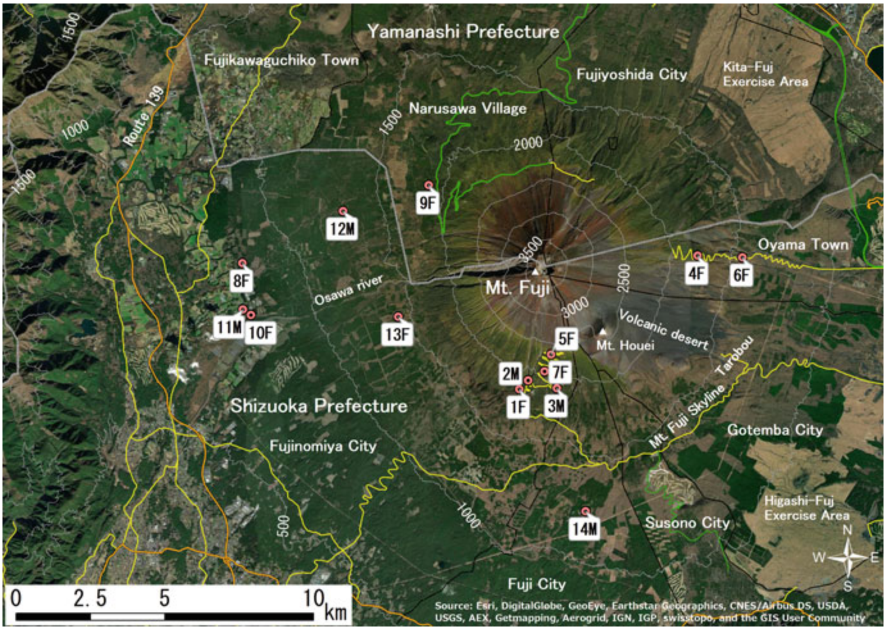
Mt. Fuji is a volcanic cone, mainly composed of basaltic ejecta. It is characterized by its gentle lateral slope, surrounded by a vast foothill area with a slight slope (Tsuya 1971). Mt. Fuji is still considered to be a young volcano that has grown to its present form in the last 10,000 years, and overall, it has only been slightly eroded. However, the local erosion of the landform has caused an array of radiating erosion valleys along the sides of the mountain (Tsuya 1971).

At the Kawaguchiko Weather Station (35.5 °N, 138.76 °E, 860 m above sea level) of the Japan Meteorological Agency (JMA), located at the northern foot of the mountain, the annual average precipitation is 1585.9 mm, the annual average temperature is 11.0 °C, and the number of snowy days is 36.7(1991–2020). At the Fuji Special Regional Meteorological Observatory (35.36 °N, 138.73 °E, 3775 m a.s.l.), located at the summit of the mountain, the average annual temperature is—5.9 °C (1991–2020), and the average number of snowy days is 108.4 (1991–2004). The amount and duration of snow cover on Mt. Fuji have not yet been reported from an aerial perspective. However, Nashimoto et al. (2016) performed a study on the maximum annual snow depth along the altitudinal gradient of the slopes of Mt. Fuji and analyzed its variation over 16 years. The results of this study show that the maximum annual snow depth (mean ± SD) in the lower part of the subalpine zone (four points in each of the four directions at elevations of 1600–1900 m; every 100 m) was 85 ± 51 cm on the east, 68 ± 51 cm on the north, 44 ± 49 cm on the south, and 21 ± 18 cm on the west. Mt. Fuji experiences many sunny days and little snowfall in winter, especially along the western slopes up to the southern foot of the mountain.

According to the vertical pattern of vegetation on Mt. Fuji, there are a *Camellia japonica* region consisting of evergreen broad-leaved forests at an elevation <800 m a.s.l., a *Querco-Fagetea crenatae* region consisting of deciduous broad-leaved forests at 800–1600 m a.s.l., a *Vaccinio-Piceetea* region (subalpine coniferous forest) at an elevation >1600 m a.s.l., and vegetation on sand and gravel of volcanic barren land from the forest limit around 2400 m to the vegetation limit around 3000 m a.s.l. (Miyawaki 1971). On the southeastern slope of the mountain, the 1707 eruption of Mount Houei lowered the volcanic wasteland to about 1300 m a.s.l.; the larch (*Larix kaempferi*) grows in a dwarf form as the pioneer woody plant around the forest limit. In terms of compensatory vegetation, planted forests occupy a large area of the entire mountain, especially in the Quercus-beech class, where Japanese cypress (*Chamaecyparis obtusa*) and Japanese cedar (*Cryptomeria japonica*) plantations are common. On the northern slopes of the area, larch plantations are common, followed by *Abies homolepis* (Miyawaki 1971). The Self-Defense Forces training grounds at Higashi-Fuji and Kita-Fuji are vast *Miscanthus sinensis* grasslands, and the pastures are widely distributed at the western foot of Mt. Fuji.

13.3 Methods

In November and December 2010, we captured 14 sika deer from various locations at the foothills of Mt. Fuji (Fig. 13.1). First, we searched for the sika deer while driving in a car at a low speed. Upon spotting individuals by the side of the road, we



Source: Esri, DigitalGlobe, GeoEye, Earthstar Geographics, CNES/Airbus DS, USDA, USGS, AEX, Getmapping, Aerogrid, IGN, IGP, swisstopo, and the GIS User Community

Fig. 13.1 A map showing the capture sites for tracking sika deer in Mt. Fuji. Source: Esri, DigitalGlobe, GeoEye, Earthstar Geographics, CNES/Airbus DS, USDA, USGS, AEX, Getmapping, Aerogrid, IGN, IGP, swisstopo, and the GIS User Community used a tranquilizer gun to fire a syringe containing a mixture of ketamine hydrochloride and xylazine hydrochloride to immobilize them. Thereafter, we fitted the immobilized sika deer with both a GPS collar (Tellus Basic or Satellite, Followit AB, Lindesberg, Örebro, Sweden) and a VHF collar (LT-01, 0.14 kg, Circuit Design, Inc., Azumino City, Nagano, Japan). Adult males were fitted with a Tellus Basic 2D (weight: 0.85 kg) or Tellus Satellite 2D (weight: 1.3 kg) collar with a large battery capacity, while females and young males were fitted with a relatively light Tellus Basic 1D (weight: 0.65 kg) collar, such that the total weight of the collar did not exceed 2% of their body weight. Finally, external measurements and body mass of the sika deer were recorded, and an antagonist (atipamezole hydrochloride) was administered to stimulate arousal and release the individuals.

Collars with 2D batteries were scheduled to record the position of the deer every 45 to 60 min, while the collars with 1D batteries were scheduled to record the individual's position every 90–120 min. Additionally, the GPS collars attached to the deer that were captured from a pasture at the western foot of Mt. Fuji were set to high-frequency intervals for 4 days, particularly from the sixth to the ninth of each month. During this period, the collar attached to No. 8 (female) was scheduled to record her position every 15 min, while the collar attached to No. 11 (male) was scheduled to record his position every 5 min. We believed that this would allow us to carry out an approximate estimation of the daily migration route as well as the distance traveled by the individual.

The beacon wave transmitted by the VHF collar was received later via the directional antenna, and the location data acquired by the GPS collar were collected by approaching the tracked individual. We used a Tellus satellite, which has the ability to send location information via a communication satellite periodically.

From the location data obtained, GIS software (ArcGIS Desktop ver.9 and ver.10 (with Extension: Spatial Analyst), ESRI, Redlands, California, United States) was used to extract the data with an elevation error of $\leq$30 m and a horizontal dilution of precision (HDOP) ≤ 4 as high-precision positioning points (Chap. 15). The home range size was determined with the fixed kernel method (Worton 1989) using the Home Range Tools for ArcGIS (Center for Northern Forest Ecosystem Research 2007) based on the high-precision positioning points that were separated by more than 2 hours. Since the action area of the sika deer can be obtained by analyzing a large number of highly accurate positioning points, the bandwidth was set to 20 m to avoid overestimation of the action area owing to the possibility of considering extended areas outside the used positioning points. The home range area of the collared sika deer was determined using the 95% fixed-kernel density estimates (KDE), whereas the 50% KDEs for each deer represented its core area. Moreover, a "seasonal home range" was defined as an area within the home range where seasonal shifting occurs with respect to the use of a location, and the "seasonal home range" of one sika deer did not overlap with that of the others. The horizontal distance between two high-precision points during the high-frequency position data collection was calculated using GIS software according to the time of positioning, and the results were tabulated daily. Additionally, we compared the high-precision positioning points with the GIS data of the 1:25,000 scale vegetation map created during the seventh Basic Survey on Nature Conservation (Ministry of Environment 2013) and extracted information regarding the time of pasture use by the sika deer.

Fourteen animals (five males and nine females) were captured (Fig. 13.1). Individuals using the pasture (No. 8 adult female, No. 10 adult female, and No. 11 adult male) were captured at an altitude of 760–830 m a.s.l., whereas the others were captured at 1200–2300 m a.s.l. Eight of the nine captured females (except for No. 9) exhibited milk secretion, indicating that they were nursing calves. Incidentally, two adult females (No. 1 and 5) died within 1 day of release and were excluded from the analysis. Moreover, one male (No. 12) was a juvenile weighing 28 kg, and hence, he was not collared. Therefore, 11 sika deer (four males and seven females) were finally tracked, and the obtained data were used for analysis (Table 13.1).

The GPS collar attached to adult male No. 3 malfunctioned, i.e., its activity sensor stopped working, positioning data were recorded at intervals different from the set schedule, etc. from November 15, 2010, and it eventually dropped out on January 7, 2011. Adult female No. 10 was killed by hunting on January 16, 2011, and adult females No. 4 and 7 died of unknown cause in late March 2011, i.e., 4 months after the tracking began. The GPS collar (Tellus Satellite 2D) attached to adult male No. 14 was dropped after 182 days since the tracking began, and it was recovered to be reused for deer from another area. The remaining six animals, namely, young male No. 2, adult female No. 6, adult female No. 8, adult female No. 9, adult male No. 11, and adult female No. 13 were tracked for more than 1 year. Eventually, all the GPS collars were dropped, but we managed to recover them.

13.4 Results and Discussion

13.4.1 Home Range

The three males (No. 2, 11, and 14) that were tracked for more than 180 days had a home range area of 259.6 ± 127.5 ha (mean ± SD) and a core area of 40.5 ± 27.2 ha (Table 13.1). The four females (No. 6, 8, 9, and 13) that were tracked for more than 1 year had a home range of 147.5 ± 59.9 ha and a core area of 21.4 ± 13.1 ha. Although not statistically significant (Mann-Whitney's U test, $P > 0.1$), it was observed that the males usually had a larger home range than that of the females. A similar study was conducted on a non-seasonal migratory population in the western region of Shizuoka Prefecture. However, the home range of these female sika deer was twice as large as that of the females ($n = 7$) they observed (home range of 73.0 ± 30.4 ha) (Chap. 15).

Table 13.1 Date of capture, tracking status, and home range size of sika deer in Mt. Fuji, 2010–2012

ID	Date of capture	Tracking days	Sex and age	Body mass (kg)	Total points	High accuracy positioning ratio (%)	Home range size(ha)		Notes
							95% kernel	50% kernel	
2M	Nov 2, 2010	606	YM	41	5467	49	235.8	34.5	
3M	Nov 3, 2010	66	AM	72	594	55	25.7	4.7	GPS collar failure
4F	Nov 3, 2010	142	AF	62	2091	53	149.0	19.1	Death
6F	Nov 4, 2010	597	AF	52	7862	42	229.1	38.9	
7F	Nov 9, 2010	134	AF	54	1495	68	30.6	4.3	Death
8F	Nov 11, 2010	430	AF	63	10202	54	152.8	23.6	Use pastureland
9F	Nov 11, 2010	540	AF	49	6470	15	116.2	9.2	
10F	Nov 12, 2010	104	AF	62	1455	52	72.7	13.0	Use pastureland Capture (hunting)
11M	Nov 30, 2010	450	AM	87	23405	56	397.3	70.2	Use pastureland
13F	Dec 2, 2010	530	AF	54	6368	32	91.8	13.8	Use pastureland only in spring
14M	Dec 3, 2010	182	AM	84	4399	46	145.6	16.8	Attach Tellus satellite

YM yearling male with one point antler, *AM* adult male with four points antler, *AF* adult female ≥2 years old

13.4.2 Movement Pattern

The four females that were tracked for more than a year exhibited an average elevation difference of 1224 ± 528 (±SD) m within their home range. Adult female No. 13, which showed the largest elevation difference (approximately 2000 m) within the home range, grazed in the pastures at 729 m in spring and moved to the upper subalpine zone at 2706 m in summer (Fig. 13.2). We speculated that the home ranges of the sika deer spanned different elevations in Mt. Fuji because they can easily move to different heights and utilize the resources in various environments at any time due to the concentric arrangement of the vegetation from the hilly areas to the alpine zones (Fig. 13.3).

Of the 11 animals that were finally tracked in this study, 10 animals (except No. 10 that was killed by hunting; tracked for 104 days) were confirmed to exhibit seasonal movements that changed their home ranges (Fig. 13.3). Of these, two males (No. 3 and 14) and three females (No. 8, 9, and 13) were confirmed to have migrated back and forth across the border between Shizuoka and Yamanashi prefectures. Moreover, five of the ten seasonal migrants (No. 3, 4, 6, 8, and 14) were confirmed to have migrated along the contour lines. In particular, No. 4, 6, and 14 passed through a narrow area named Tarobou between the volcanic desert and the Mt. Fuji Skyline (Fig. 13.3). In addition, five animals (No. 2, 4, 6, 7, and 14) moved to the southern foothills of Mt. Fuji (1000–1500 m above sea level in Fuji City and Susono City) during winter and used it as an overwintering site (Fig. 13.3).

The home ranges of the adult males (No. 3 and 11) were separated during the breeding (September to November) and non-breeding (December to August) seasons. Adult male No. 11 used the pastures at the foot of Fujinomiya City on the west side of Mt. Fuji in winter and spring, but it moved to Hitoana and Awakura, Fujinomiya City, in summer and autumn (Fig. 13.3). On Route 139, which runs

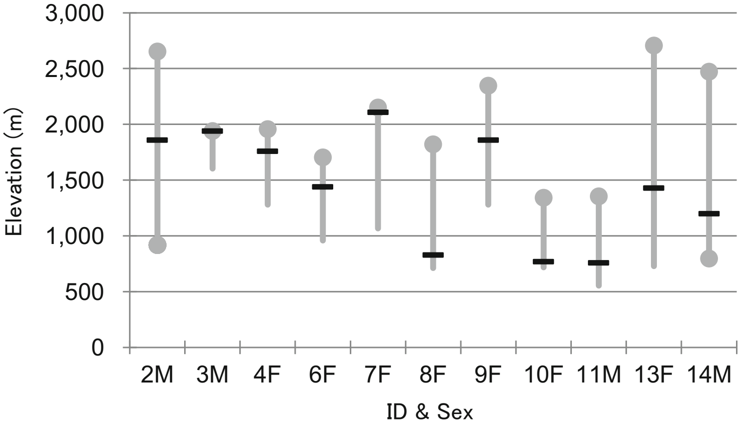


Fig. 13.2 Range of elevation used by tracking sika deer. (−) indicates the elevations of the capture sites

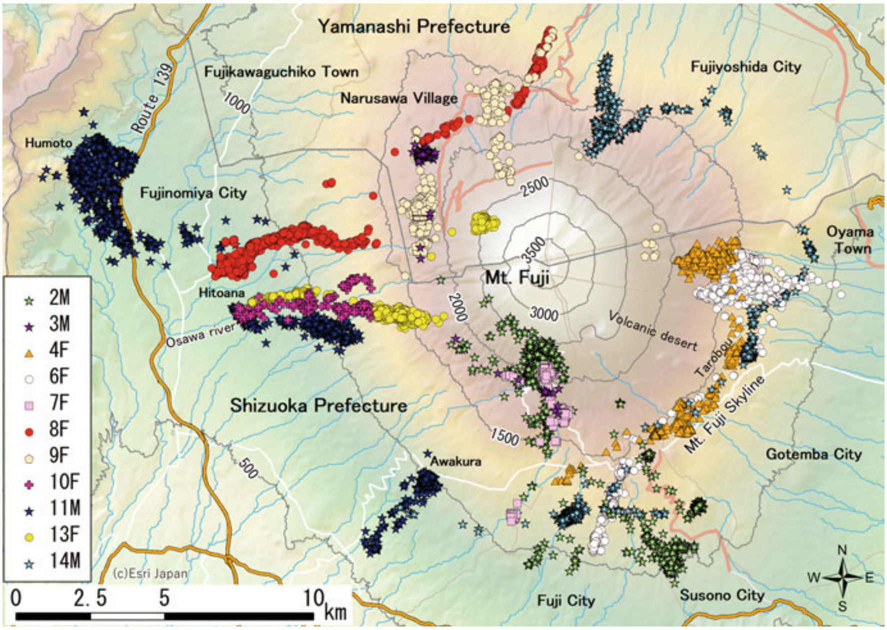


Fig. 13.3 A map showing the movement ranges of 11 tracking sika deer in Mt. Fuji

north-south through Fujinomiya City, Shizuoka Prefecture, collisions between automobiles and sika deer have become a problem. The male deer migrate across the road from the west toward Mt. Fuji for mating, and when the mating season is over, they cross the road again to return to their non-breeding area, which may lead to a high number of vehicular accidents.

Six sika deer individuals (No. 6, 8, 9, 10, 11, and 14) were found to have a vertical home range orthogonal to the contour line (Fig. 13.3). It is possible that the finely formed radial valleys around the mountain peaks restrict the behavioral area of the sika deer, resulting in the formation of such a vertical home range.

We observed temporal changes in the elevation as well as the latitude of the sites used by the ten seasonal migrants (Fig. 13.4). The time wherein a large change occurred in the elevation or latitude of an individual deer was considered as its "migration period." Incidentally, young male No. 2, which was at a higher elevation on the southern slope, and adult females No. 4 and 6, which were on the eastern slope, migrated southward in late December 2010. It is considered that they moved to areas with less snow cover for overwintering. At the same time, adult female No. 7 that had been using the southern slopes at approximately 2000 m also changed its habitat use, thereby expanding its range of activity around 1650 m and using areas at lower elevation since February 2021.

In the winter of 2010–2011, snowfall of $\geq$10 cm was recorded at the Kawaguchiko Weather Station, located at 860 m above sea level at the northern foot of Mt. Fuji, on February 14 (25 cm) and March 7 (31 cm); however, the snow

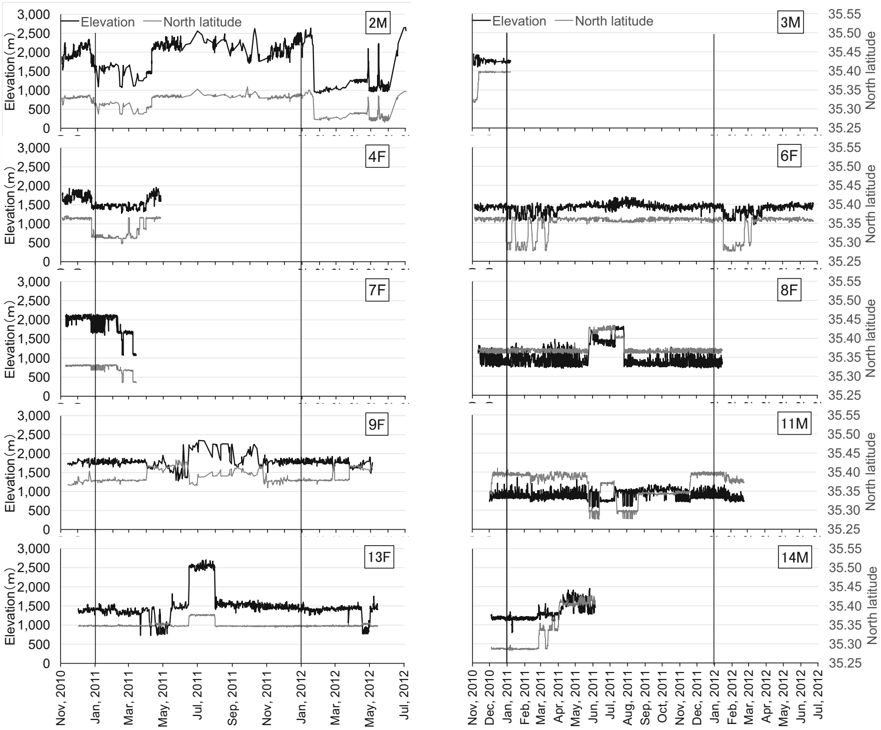


Fig. 13.4 Changes in elevation and latitude associated with the ten migrants sika deer

cover did not persist for more than 5 days. The timing of these two snowfalls coincided with the southward movements of sika deer No. 2, 4, 6, 7, and 14. The remaining five deer (No. 3, 8, 9, 10, and 11) maintained their sphere of activity on the western slope and did not migrate southward or to lower elevations during the winter.

Incidentally, adult female No. 8 left the pastures at the western foot of the mountain for nearly 2 months, from late May to late July 2011, and stayed at a slightly higher altitude at the northern foot of Mt. Fuji (Fig. 13.4). Similarly, adult female No. 9 moved to the northern foot of the mountain in April and used it until October 2011; furthermore, in the latter half of June, it used the eastern slope at an altitude of approximately 2200 m. The adult female No. 13 used the pastures at a lower elevation for a short time between late March and early May in 2011 as well as 2012, and conversely, from the latter half of June to the end of July 2011, it stayed at an elevation of approximately 2500 m in the alpine zone. The temporary use of pasture by adult female No. 13 in spring was in accordance with the results of a light census that was conducted from October 2010 to January 2012 at the western foothills of Mt. Fuji; its results showed that the number of sika deer increased in pastures between March and April, and the amount of grass damage was also high between March and May (Ohtake et al. 2012a, b).

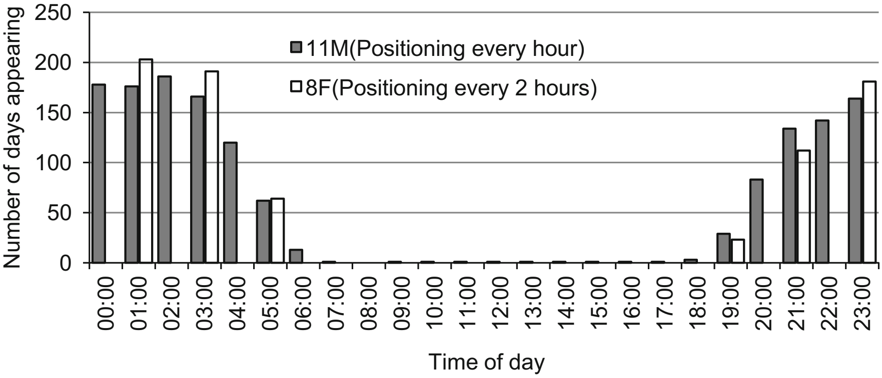


Fig. 13.5 Time of day when the two sika deer (ID: 8F and 11M) used pastureland at the western foot of Mt. Fuji

Adult female No. 8 and adult male No. 11 were dependent on the pastures for a long time, and throughout 2011, they appeared in the pastures for 238 and 207 days, respectively (Fig. 13.5). However, the adult female No. 8 did not use the pasture for 62 days between May 25 and July 25, and the adult male No. 11 did not use the pasture for 104 days, specifically from June 17 to July 4, July 11 to 24, and August 12 to October 25. The absence of adult female No. 8 from the pasture may be attributed to her migration for birthing and subsequent parental activities. Similarly, the absence of adult male No. 11 may be due to his engagement in mating activities between August 12 and October 25. Both these individuals spent a large amount of time in the meadows between 23:00 and 03:00 h. The use of pastures by sika deer has been reported in many places (Kamei et al. 2010; Iijima 2018; Hata et al. 2019). This reduces the pasture yields for the livestock, thereby causing direct damage to the livestock industry. Moreover, the use of high-nutrient pastures by sika deer may contribute to their population growth (Iijima et al. 2013; Iijima and Ueno 2016).

The distance traveled per day by adult female No. 8 and adult male No. 11 was classified into two groups, namely "pastureland use days" and "pastureland non-use days" (Fig. 13.6). The average distance traveled on the days when pastures were used was 5647 m for adult female No. 8 and 5454 m for adult male No. 11, whereas the average distance traveled on days when pastures were not used was 3057 m for No. 8 and 4320 m for No. 11. There was a significant difference (Mann-Whitney's U test, $P < 0.01$) between the distances traveled on pastureland use and non-use days. It was clear that the distance traveled per day was higher on the days when the pastureland was used than on the non-use days owing to the long commute between the forest and the pasture.

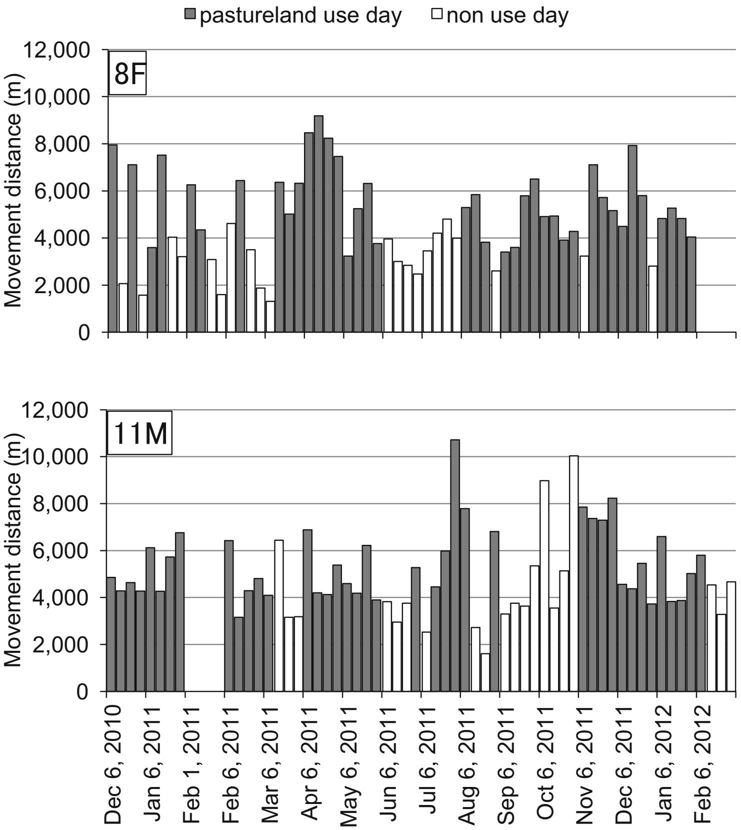


Fig. 13.6 Daily movement distances of the two sika deer (ID: 8F and 11M) (pastureland use days and non-use days) at the western foot of Mt. Fuji

13.5 Conclusion and Management Implication

The behavioral patterns of the sika deer around Mt. Fuji were influenced by the topographic and the meteorological features of Mt. Fuji, such as its existence as an independent peak with a high elevation and little snow cover in winter and the presence of pastureland along its foothills. These environmental features promote vertical and horizontal migration patterns, and many individuals migrate along the contour lines owing to the topographic simplicity. In addition, we observed that the presence of valleys restricted migration within the seasonal home range, and it occurred in a direction directly parallel to the contour lines, which tended to form a vertical sphere of activity. Therefore, to start population management in a new area and realize efficient culling, it is essential to conduct preliminary research on the characteristics of diurnal behavior patterns of the local population and the timing of their migration, as shown in this study.

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Chapter 14
Movement Patterns of Sika Deer in Western Japan

Noriko Yokoyama, Shin'ichiro Hamasaki, and Aki Mitsuhashi

Abstract We analyzed the home range of deer in western Japan. We collected data on 120 GPS-collared deer from Kinki, Shikoku, and Kyushu. The home range size in western Japan was smaller than that of deer in eastern and northern Japan. The percentage of individuals that made seasonal movements in western Japan was 20%. The percentage of seasonal migrants in collared deer varied regionally. The proportion of seasonal migrants was higher in areas with more snow accumulation. As the period during which the snow depth exceeded 50 cm became longer, the proportion of seasonal migrants increased. The migration distance ranged from 1.9 to 14.3 km, which was shorter than those in eastern and northern Japan. Further, individuals that use deciduous broad-leaved forests as their summer habitat tended to migrate seasonally, while deer who used evergreen broad-leaved forests tended to be more sedentary. Vegetation and topography in western Japan differ significantly from those in eastern and northern Japan, and deer behavior is also characteristic and unique to western Japan.

14.1 Introduction

In recent years, increase in the population of sika deer has had a significant impact on forest ecosystems, such as decline in understory vegetation (Kabaya 1988; Hasegawa 2000; Ohashi et al. 2007; Tsujino et al. 2007; Murata et al. 2009; Hattori et al. 2010) and soil erosion (Furusawa et al. 2003; Yanagi et al. 2008). Therefore, in

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N. Yokoyama (✉)
Wildlife Management Office Inc., Hiroshima Branch, Onomichi, Hiroshima, Japan
e-mail: nori_yokoyama@wmo.co.jp

S. Hamasaki
Wildlife Management Office Inc., Hachioji, Tokyo, Japan
e-mail: sin-hamasaki@wmo.co.jp

A. Mitsuhashi
Wildlife Management Office Inc., Kansai Division, Kobe, Hyogo, Japan
e-mail: mitsuhashi@wmo.co.jp

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2013, as a drastic control measure, the national government set a goal to halve the population of sika deer estimated in 2011 by 2025. This measure promoted the deer-capturing business. However, since the number of hunters in Japan has decreased, there is a need to develop more efficient capturing methods and conventional practices. Therefore, behavioral characteristic surveys of sika deer were conducted in various national and local governments.

Since the 1980s, surveys on the behavioral characteristics of sika deer have been conducted using very high frequency (VHF) transmitters, mainly in the Kanto and northward (e.g., Maruyama 1981; Furubayashi et al. 1987; Nagata et al. 1994; Yamazaki and Furubayashi 1995; Borkowski and Furubayashi 1998; Sakuragi et al. 2002; Nagata 2005), which replaced GPS collars in the 2000s and used extensively (e.g., Takii et al. 2012a). At that time, the surveys using GPS collars expanded in western Japan as national and local government projects since the increase in the density of sika deer has been having a substantial impact on forest vegetation (Tsujino et al. 2007; Murata et al. 2009; Hattori et al. 2010; Matsui et al. 2011).

Previous surveys reveal two contrasting movement patterns: seasonal migrants in northern and eastern Japan and sedentary individuals in western Japan (Yabe and Takatsuki 2009). It is inferred that in northern and eastern Japan, sika deer migrates to wintering grounds during winter (Miura 1974; Maruyama 1981) due to the presence of snow that restricts their behavior (Takatsuki 1992) and the scarcity of food resources. On the other hand, in western Japan, since there are many evergreen broad-leaved forests and food resources do not change much between summer and winter, there are many sedentary individuals (Yabe and Takatsuki 2009).

Some studies have reported that the snow depth of 50 cm or more restricted sika deer movements and sika deer avoided these areas (Tokita et al. 1981; Takatsuki 1992). In cervids inhabiting high latitudes such as white-tailed deer (*Odocoileus virginianus*) and roe deer (*Capreolus capreolus*), their migration patterns from summer to winter habitats are mainly attributed to snow depth (Tierson et al. 1985; Mysterud 1999; Sabine et al. 2002; Brinkman et al. 2005; Ramanzin et al. 2007) and low temperatures (Nelson 1995).

In the case of sika deer, the formation of wintering grounds for seasonal migration has been reported in snowy and high-altitude areas in northern and eastern Japan such as Hokkaido (Uno and Kaji 2000; Igota et al. 2004), Mt. Goyo (Takatsuki et al. 2000), Nikko (Maruyama 1981), Okuchichibu (Takii et al. 2012a), and Kirigamine (Takii et al. 2012b). Although the presence of seasonal migrants in western Japan has also been confirmed, only a few reports are available in limited areas such as Mt. Hyonosen range (Morimitsu et al. 2019), Odaigahara (Maeji et al. 2000), and the central mountains of Kyushu (Yabe et al. 2001). While the seasonal migration in Mt. Hyonosen range and Odaigahara was reported to be caused by snow cover, the movement of males during the breeding season in the mountains of Kyushu has no reference to the effects of snow cover.

Although only a few comprehensive reports on the behavioral characteristics of sika deer in western Japan are available, the number of survey cases conducted by governmental countermeasure projects has increased in recent years. However, in many of these cases, and since the number of individuals surveyed is small, the reports are only fragmentary. Therefore, in this paper, to elucidate the behavioral characteristics of sika deer in western Japan, we have aggregated and analyzed these survey data focusing on the home range area, seasonal migration, and habitat used compared with the previous studies in northern and eastern populations.

14.2 Survey Area

Western Japan refers to the region west of Kinki that includes Kinki, Chugoku, Shikoku, and Kyushu (Fig. 14.1). In this survey, data were collected only from three regions: Kinki, Shikoku, and Kyushu.

There are no mountains higher than 2000 m in western Japan; the highest peak is Mt. Ishizuchi in Shikoku with an elevation of 1982 m. The highest mountain range in Kinki is the Kii Mountains with an elevation of 1800 to 1900 m. The mountains of central Kyushu are the highest with an elevation 1500 to 1800 m, and the only mountain over 1800 m is the Yakushima.

Japan is a long country extending from north to south, ranging from temperate humid to subarctic continental humid climates, and western Japan belongs to the former. The monthly average temperature varies between 5 and 30 °C in Fukuoka, and the hottest days are in August with temperatures exceeding 35 °C at times. Annual precipitation varies between regions from 1000 mm to over 3000 mm. The

Fig. 14.1 Study areas in western Japan

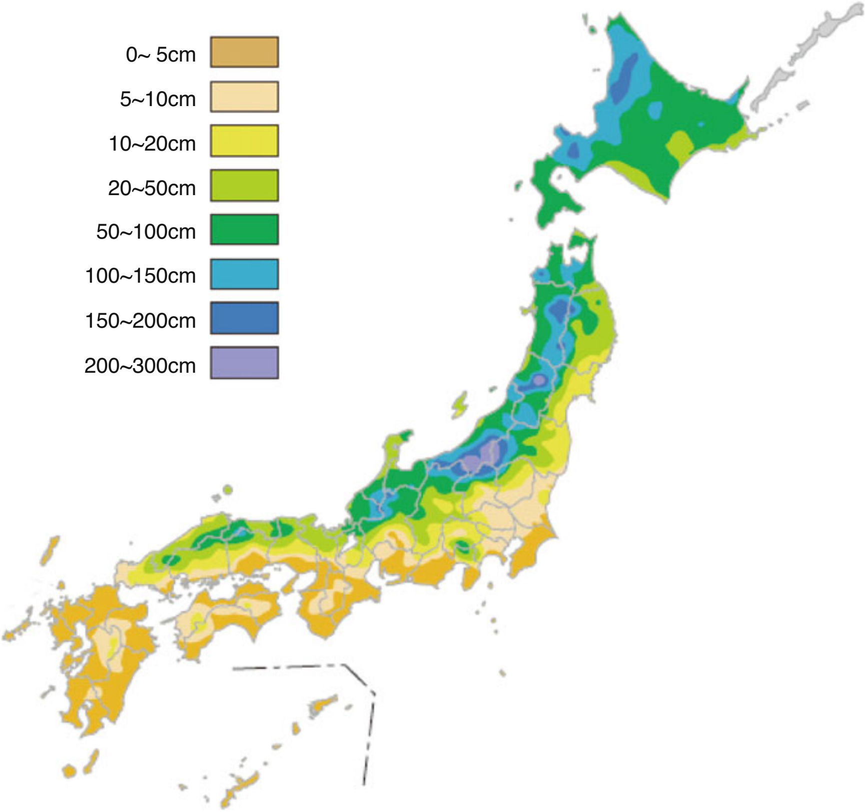

Fig. 14.2 Maximum snowfall depth in Japan (average values from 1971 to 2000) (Modified from the Japan Climate Map FY2000)(Japan Meteorological Agency 2012)

amount of snowfall tends to be more on the Sea of Japan side and less on the Pacific side. While there are many areas with rainfall exceeding 100 cm in northern and eastern Japan, the rainfall in western Japan varies between 50 and 100 cm in some mountainous areas and 0 to 5 cm on the plains. It is an area of little snowfall and almost no snow cover (Japan Meteorological Agency) (Fig. 14.2).

While northern and eastern Japan have many deciduous broad-leaved forests dominated by beech (*Fagus crenata*) and Mongolian oak (*Quercus crispula*), western Japan has many evergreen broad-leaved forests dominated by *Castanopsis* spp. and Japanese emperor oak (*Quercus dentata*), and deciduous broad-leaved forests in high-altitude areas (Fig. 14.3).

Another characteristic of western Japan is the large area of plantation forests that accounts for half of the afforested area in Japan. The area of plantation forests is 27% in Hokkaido, 40% in Tohoku, 45% in and Kanto, 39% in Chubu, and 50% in western Japan (51%, 41%, 60%, and 53% in Kinki, Chugoku, Shikoku, and Kyushu, respectively). Japanese cedar (*Cryptomeria japonica*) and Japanese cypress

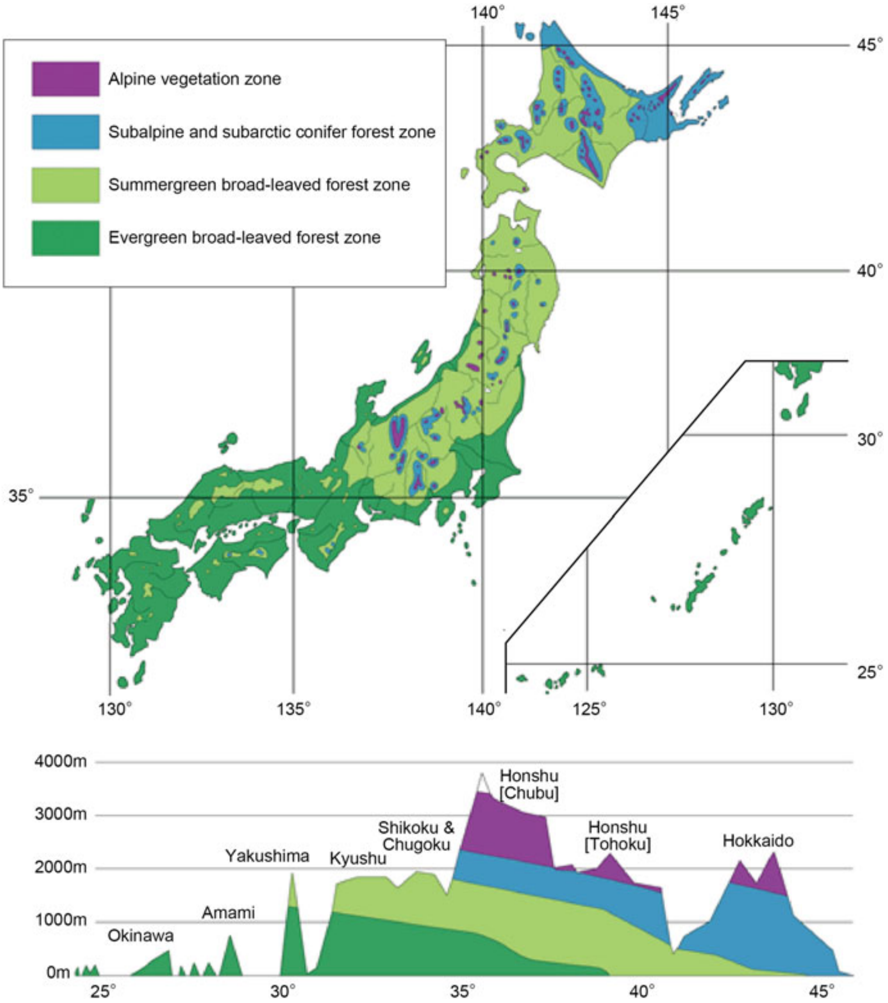

Fig. 14.3 Vegetation distribution in Japan. Modified from Japanese Vegetation by Miyawaki (1977)

(*Chamaecyparis obtusa*) account for 70% or more of the plantation forests in Japan, except for Hokkaido. The proportion of evergreen conifers, such as Japanese cedar and cypress, in the plantation forests is as high as 93%, 94%, and 93% in Kinki, Shikoku, and Kyushu, respectively (Forestry Agency Private Forest Department Planning Division 2018).

14.3 Methods

14.3.1 Data Collection

14.3.1.1 GPS Positioning Data

We collected the positioning data of GPS-collared sika deer in western Japan from the national and local government projects from 2009 to 2019. Inquiring the related organizations in Kinki, Shikoku, and Kyushu, we obtained data on 145 deer in total. The northernmost area was Mt. Ibuki, Shiga Prefecture (35°25′N 136°24′E), and the southernmost was Yakushima, Kagoshima Prefecture (30°13′N 130°30′E). The number of surveyed individuals is shown for each attribution of collected data and survey year (Table 14.1). Among the collected data, those with a tracking period of less than 90 days were excluded from the analysis. Further, 3D data with high GPS positioning accuracy were used for analysis; individuals whose 3D data was less than 1 point per day were excluded from the analysis.

14.3.1.2 Environmental Data

To analyze the habitat used by sika deer and the factors of its seasonal migration, we used the vegetation and snow depth data. For the vegetation, we used the high-resolution land use/land cover map (resolution 10 m) provided by the Earth Observation Research Center of the Japan Aerospace Exploration Agency (JAXA) (2018). This data classifies the land use into 10 types: water, urban and built-up, rice paddy, crops, grassland, deciduous broad-leaved forest, deciduous conifer forest, evergreen broad-leaved forest, evergreen conifer forest, and bare land.

For the snow cover data, we used the Agro-Meteorological Grid Square Data, NARO (Ohno et al. 2016). This data was created in units of about 1 km^2 (reference region mesh) by interpolation based on various meteorological data such as AMeDAS, taking into consideration the altitude.

14.3.2 Analysis

14.3.2.1 Home Range

The home range was estimated using two methods: minimum convex polygon (MCP) and fixed kernel (Worton 1989). For both methods, the “adehabitat” package for the R software (ver.4.0.3) was used. The home range was estimated by 90% home range of MCP and fixed kernel (hereafter referred to as “MCP90HR” and “FK90HR”, respectively) using all data during the follow-up period. For the core area, 50% home range was calculated using fixed kernel (hereafter referred to as the “core area”). The estimated home range was converted into a “shape file,” and the

Table 14.1 Data attribution for projects using GPS collars and survey year

Data attribution	Survey year											Total
	2009	2010	2011	2012	2013	2014	2015	2016	2017	2018	2019	
The Forestry Agency's Kinki-Chugoku Regional Forest Office								2	3	1		6
The Forestry Agency's Kyushu Regional Forest Office		9	42	2	8	7	3	5	1			77
Ministry of the Environment: Chugoku and Shikoku	5	1	2									8
Mie Prefecture						1	2		5	2	1	11
Shiga Prefecture	10	3	1	7	4	4		4	2			35
Tokushima Prefecture						2	2					4
Fukuoka Prefecture									4			4
Total	15	13	45	9	12	14	7	11	15	3	1	145

home range was analyzed using ArcGIS (ver.10.5.1). For the individuals for whom multiple core areas were formed due to seasonal migration or the like, estimation was performed by dividing the period into before and after migration.

The statistical difference in home range areas between sexes was examined by a Mann-Whitney U in Kinki and Kyushu and a Welch t-test in Shikoku. The Steel-Dwass test was used to examine the difference of home range areas between three regions. The significant level was set as 0.05.

14.3.2.2 Determination of the Presence or Absence of Seasonal Migration

To identify the individuals that have migrated, the core area was estimated for the entire survey period, and the ones in which multiple core areas were formed were extracted. In addition, the positioning data of each individual was classified per month, and the presence or absence of migration was confirmed from the monthly position point distribution. Further, the core areas were estimated for the period before and after the migration; individuals with no overlapping core areas (before and after migration) were regarded as seasonally migrating. The distance between the centers of gravity of the estimated core areas before and after the migration was calculated by ArcGIS.

14.3.2.3 Habitat Use

The snow depth of the center of gravity of the MCP90HR of the individuals for whom the tracking period included winter were extracted and classified into 50 cm of snow depth classes. The vegetation from the GPS data points was extracted using the high-resolution land use/land cover map (resolution 10 m) and analyzed. A Pearson's chi-squared test was used to compare the vegetation used by sedentary deer with migratory individuals.

14.4 Results

14.4.1 Information of Analyzed Individuals

Among the data collected from the GPS-collared sika deer ($n = 145$), three deer had less than one point of positioning data per day. The number of deer with a tracking period of more than 90 days used in the analysis was 120 individuals (with male: female ratios of 8:37, 3:3, and 21:48 in Kinki, Shikoku, and Kyushu, respectively). The total individuals with a tracking period of 180 days or more were 69 (male: female ratios of 6:23, 3:1, and 9:27 in Kinki, Shikoku, and Kyushu, respectively). Only 32 individuals with a tracking period of 300 days or more were found (male:

Table 14.2 Number of sika deer surveyed using GPS collars by tracking period

Area	Sex	Number of sika deer by the tracking period					
		<90 days	90–179 days	180–299 days	≥300 days	Total of ≥90 days	Total of ≥180 days
Kinki	Male	3	2	2	4	8	6
	Female	4	14	6	17	37	23
Shikoku	Male	1	0	0	3	3	3
	Female	3	2	0	1	3	1
Kyushu	Male	3	12	9	0	21	9
	Female	8	21	20	7	48	27
Total		22	51	37	32	120	69

female ratios of 4:17, 3:1, and 0:7 in Kinki, Shikoku, and Kyushu, respectively) (Table 14.2). Since long-term surveys have not been conducted in Shikoku and Kyushu, only a few individuals had a tracking period of 300 days or more.

14.4.2 Home Range Size

Table 14.3 shows the average home range and core areas of sika deer in Kinki, Shikoku, and Kyushu. The home range size of individuals with a tracking period of 90 days or more was the largest for males in Kinki with 5.90 km^2 in MCP90HR and 3.84 km^2 in FK90HR. The home range of females was also the largest in Kinki, with 2.09 km^2 and in MCP90HR. Males had a larger core area size (FK50) than females in Kyushu.

Fig. 14.4 shows the home range size by region and by sex. Comparing the home range size between the sexes by region, there was a significant difference between Kinki and Kyushu in both MCP90HR and FK90HR, and the home range area was larger for males in both regions (MCP90HR; Kinki: $W = 254$, $p < 0.001$, Kyushu: $W = 681$, $p < 0.05$, FK90HR; Kinki: $W = 204$, $p < 0.05$, Kyushu: $W = 694$, $p < 0.05$). There was a significant difference between the core area of males and females in Kyushu, with a broader core area for males ($W = 774$, $p < 0.05$).

Comparing the regions by sex, there was a significant difference between the males in Kinki and Kyushu in MCP90HR, where Kinki showed a larger home range ($t = 2.830$, $p < 0.05$). The same was true for females; Kinki had a larger home range than Kyushu ($t = 2.810$, $p < 0.05$). In FK90HR, while there was no regional difference in males, there was a significant difference between the two regions in females, with a larger home range in Kinki ($t = 3.383$, $p < 0.01$). In the core area, while there was no regional difference in males, there was a significant difference in females, with a larger core area in Kinki ($t = 2.651$, $p < 0.05$).

Table 14.3 Average size of the home range and core areas of sika deer by tracking period in each region. MCP90 indicates 90% of minimum convex polygon, FK90 and FK50 indicate 90% and 50% of fixed kernel, respectively

		Average area (km^2)											
		Tracking period (≥90 days)				Tracking period (≥180 days)				Tracking period (≥300 days)			
Area	Sex	*n*	MCP90	FK90	FK50	*n*	MCP90	FK90	FK50	*n*	MCP90	FK90	FK50
Kinki	Male	8	5.90	3.84	0.34	6	5.26	2.54	0.24	4	5.70	1.65	0.24
	Female	37	2.09	2.01	0.15	24	2.53	1.58	0.15	17	2.11	1.27	0.14
Shikoku	Male	3	0.90	0.43	0.21	3	0.90	0.43	0.21	3	0.90	0.43	0.21
	Female	3	0.52	0.53	0.16	1	0.57	0.60	0.12	1	0.57	0.60	0.12
Kyushu	Male	21	1.92	1.54	0.25	9	1.76	1.23	0.25	0	–	–	–
	Female	48	1.56	1.37	0.13	27	0.85	0.75	0.15	7	0.32	0.32	0.09

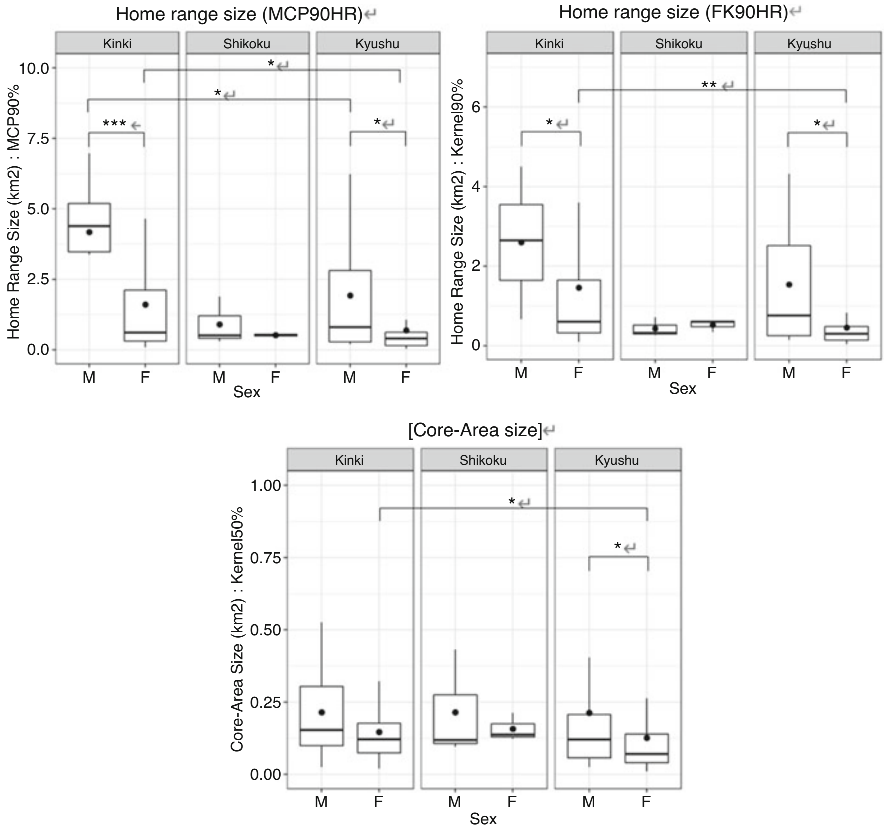

Fig. 14.4 Home range size and core area estimated using the minimum convex polygon and fixed kernel for 90% of the home range (MCP90HR and KF90HR, respectively) analyzed for individuals with a tracking period of 90 days or longer

14.4.3 Percentage of Seasonally Migrating Individuals

The percentages of seasonally migrating individuals by region were 37% and 10% in Kinki and Kyushu (Table 14.4), respectively, and no migrating individuals in Shikoku. Males migrated at a higher rate than females. Of the 120 GPS-collared sika deer, 80% exhibited sedentary behavior, and 20% exhibited seasonal migration.

In Kinki, the males migrated 1.9 to 5.9 km, with an average of 3.6 km ($n = 6$), while the females migrated 2.1 to 9.2 km, with an average of 4.3 km ($n = 11$). In Kyushu, the males migrated 3.6 to 4.0 km, with an average of 3.8 km ($n = 5$), while females migrated 2.1 to 14.3 km with an average of 7.0 km ($n = 2$).

In this survey, 7 out of 11 migratory males moved to their winter habitat around November, and the rest 4 moved during summer and autumn months. One, in the Kinki, out of four males moved to an area 5 km far from its normal habitat in May,

Table 14.4 Percentage of seasonally migrating individual sika deer by region and migration distance

Area	Sex	*n*		Ratio (%)		Migratory distance (km)	
		Sedentary	Migratory	Sedentary	Migratory	Range	Mean
Kinki	Male	2	6	25.0	75.0	1.9–5.9	3.6 ± 1.6
	Female	26	11	70.3	29.7	2.1–9.2	4.3 ± 2.1
Shikoku	Male	3	0	100.0	0.0	–	–
	Female	3	0	100.0	0.0	–	–
Kyushu	Male	16	5	76.2	23.8	3.6–4.0	3.8 ± 0.2
	Female	46	2	95.8	4.2	2.1–14.3	7.0 ± 5.3
Total		96	24	80.0	20.0	1.9–14.3	4.4 ± 2.7

Table 14.5 Number of sedentary and migratory sika deer depending on the snow depth, in Kinki, Shikoku, and Kyushu regions

Maximum Snow depth of the center of gravity of the MCP90% HR	Number of sika deer				Percentage of migratory sika deer	
	Sedentary		Migratory			
	Male	Female	Male	Female	Male (%)	Female (%)
0–50 cm	14	59	4	1	22.2	1.7
50–100 cm	5	4	2	2	28.6	33.3
100 cm–	0	2	4	6	100.0	75.0

stayed there for a month, and then returned to its normal habitat. And one male in the Kinki and two in the Kyushu moved to the unusual area in the period between September and November.

On the other hand, all collared migratory females moved from summer habitat to winter habitat between November and January. None of them moved at different times of the year as in the case of males.

14.4.4 The Effect of Snow Depth on Percentage of Seasonally Migrating Individuals

The snow depth of the center of gravity of MCP90HR and the numbers of sedentary and migrating individuals are shown in Table 14.5. In the presence of 0–50 cm snow, 22.2% of males and 1.7% of females migrated. At a snow depth of 50–100 cm, 28.6% of males and 33.3% of females migrated. On the contrary, in areas with heavy snowfall (snow depth of more than 100 cm), 100% of males and 75% of females were migratory, showing high percentage of migratory sika deer.

A previous study suggested that sika deer tended to avoid areas with more than 50 cm of snowfall for 10 days or more (Tokita et al. 1981). Table 14.6 shows the percentage of migratory sika deer, according to the three classes with more than

Table 14.6 Number of days with a snow depth of 50 cm or more and percentage of migratory sika deer, in Kinki, Shikoku, and Kyushu regions

	Number of sika deer				Percentage of migratory sika deer	
	Sedentary		Migratory			
Number of days with a snow depth of 50 cm or more	Male	Female	Male	Female	Male (%)	Female (%)
$<$10 days	16	61	5	2	23.8	3.2
10–19 days	1	1	0	0	0.0	0.0
$\geq$20 days	2	3	5	7	71.4	70.0

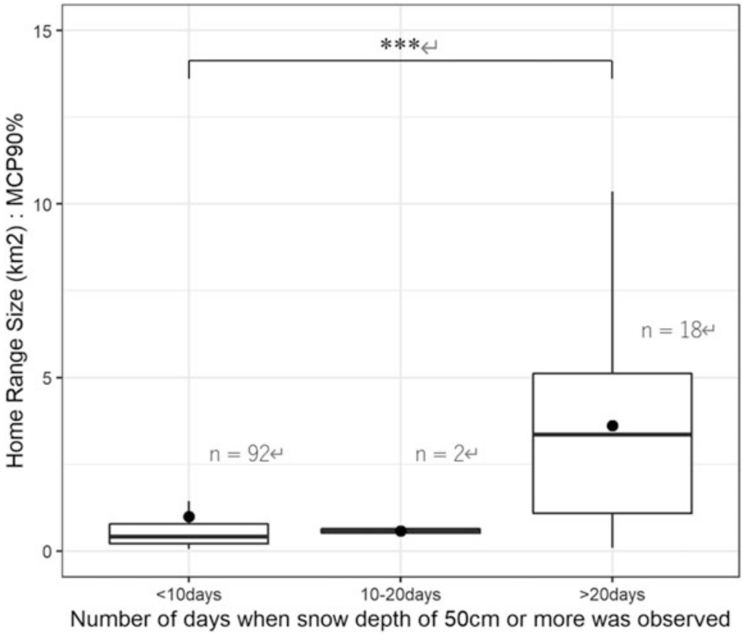

Fig. 14.5 Relationship between the number of days with a snow depth of 50 cm or more and MCP90HR area of sika deer in Kinki, Shikoku, and Kyushu regions

50 cm of snow: less than 10 days, 10 to 19 days, and 20 days or more. When the snow depth was 50 cm or more for less than 10 days, the percentage of migratory deer was 23.8% and 3.2% for males and females, respectively. When the duration of snow was for 20 days or more, 71.4% and 70.0% of males and females migrated, respectively. No migration was recorded between 10 and 19 days.

Further, the number of days on which the snow depth was 50 cm or more was compared with the home range size of MCP90HR (Fig. 14.5). The median home range (MCP90HR) for the class where the snow depth was 50 cm or more for less than 10 days was 0.42 km^2, and for 20 days or more, the median was 3.37 km^2, a significantly larger home range ($W = 313$, $p < 0.001$) than the former class.

14.4.5 Habitat Use

The vegetation types from the GPS positions were compared separately for sedentary and migratory individuals (Fig. 14.6). The sedentary individuals most often use evergreen coniferous forests compared to seasonal migrants in Kinki (with 48.3% and 51.3%, and 24.8% and 18.2% for males and females, respectively), showing a higher utilization rate (males: $\chi^2 = 874$, $p < 0.001$, females: $\chi^2 = 9624$, $p < 0.001$). Seasonal migrants utilized the deciduous broad-leaved forests more often than sedentary individuals (59.0% and 73.4%, and 42.3% and 32.2% for males and females, respectively). The utilization of the deciduous broad-leaved forests by seasonal migrants was therefore higher than that of sedentary individuals (males: $\chi^2 = 365$, $p < 0.001$, females: $\chi^2 = 14{,}475$, $p < 0.001$).

In Kyushu, evergreen coniferous forests were most often used by sedentary individuals compared to seasonal migrants (with 48.2% and 45.4%, and 32.0% and 35.7% for males and females, respectively) showing a lower utilization rate than sedentary individuals (males: $\chi^2 = 1448$, $p < 0.001$, females: $\chi^2 = 507$, $p < 0.001$). In males, there was no significant difference between the seasonal migrants and sedentary individuals for vegetation types other than evergreen coniferous forests. The evergreen broad-leaved forest utilization rate by females was 29.0% and 21.8% for sedentary individuals and seasonal migrants ($\chi^2 = 343$, $p < 0.001$), respectively. The utilization rate of deciduous broad-leaved forests was 22.4% and 37.8% for sedentary individuals and seasonal migrants ($\chi^2 = 1792$, $p < 0.001$), respectively.

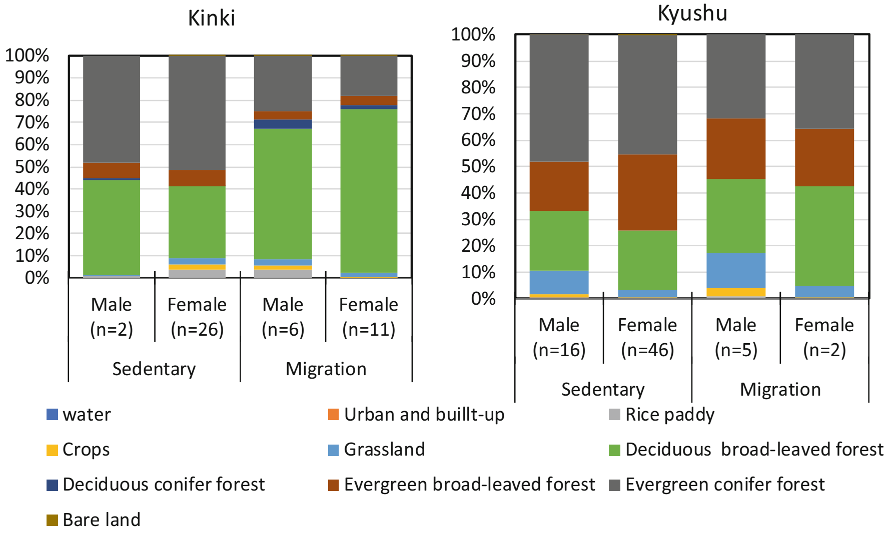

Fig. 14.6 Comparison of vegetation used by sedentary migrants of sika deer in Kinki and Kyushu regions. The percentages indicate the percentage of points of the vegetation type at the positioning point

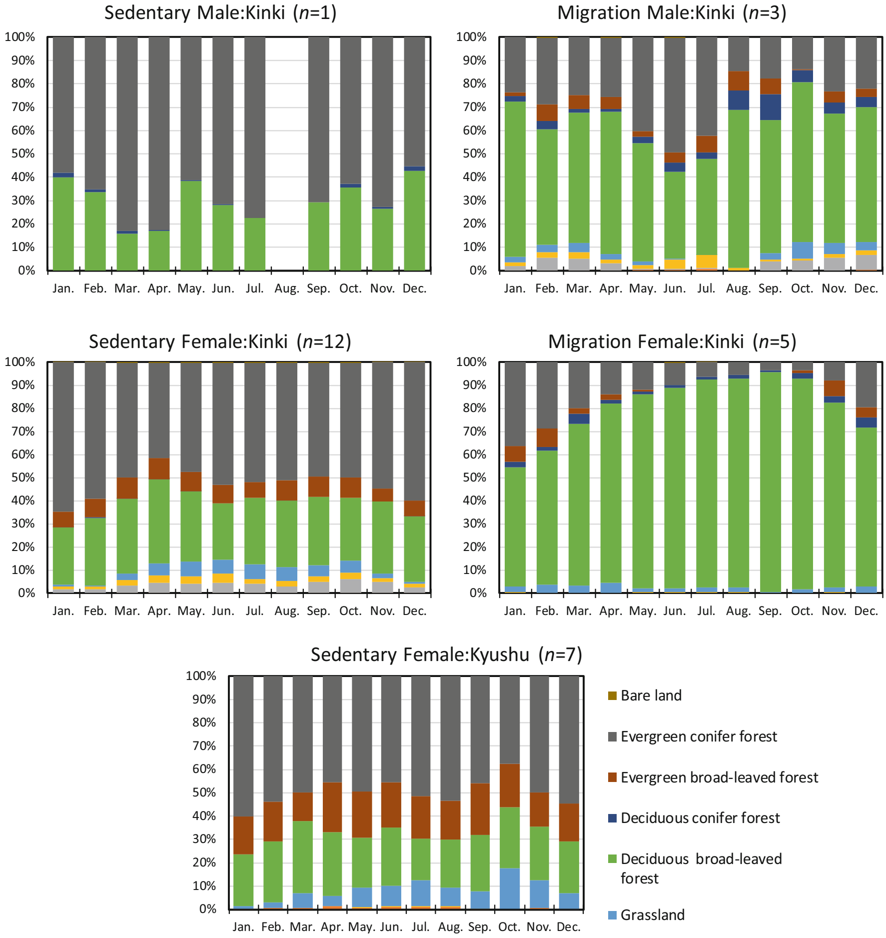

Fig. 14.7 Monthly vegetation use by sika deer by sedentary and migratory with a tracking period of 300 days or more in Kinki and Kyushu regions. The percentages indicate the percentage of points of the vegetation type at the positioning point

The monthly variation in the vegetation used by individuals with a tracking period of 300 days or more is shown in Fig. 14.7. Sedentary individuals did not show any significant change in vegetation type used throughout the year, regardless of the region or sex. However, grasslands tended to be used more frequently from April to October. Seasonally migrating males use grasslands more often between June and July. On the other hand, there was an apparent seasonal change in the vegetation type used by seasonally migrating females. While the utilization rate of deciduous broad-leaved forests was high during summer, evergreen coniferous and broad-leaved forests were mostly preferred during the winter.

14.5 Discussion

14.5.1 Home Range Size

The home range size is influenced by various factors such as the quality and quantity of food resources, density of sika deer (Takatsuki 1992), and disturbance caused by human activities such as hunting (Kamei et al. 2010). The presence or absence of seasonal migration due to snow cover, which restricts the behavior of sika deer, strongly affects the size of their home range (Takatsuki 1992; Igota et al. 2004; Takii et al. 2012a). In the results of this analysis, males showed a larger home range size and core area size than females. In general, males of sika deer are known to have a larger home range than females (Maeji et al. 2000), and the same result was obtained in this study. The percentage of seasonal migrants varied from region to region. Further, the proportion of seasonal migrants was higher in areas with more snow, and as the period during which the snow depth exceeded 50 cm became longer, the proportion of seasonal migrants increased, which affected the home range size. This result is similar to the results from other regions such as Hokkaido (Igota et al. 2004), Nikko (Maruyama 1981), Kirigamine (Takii et al. 2012b), and Mt. Hyonosen (Morimitsu et al. 2019), where snow cover is reported as one of the main causes for seasonal migration.

In terms of the size of the core area, the summer home range was 0.19 to 6.02 km^2 in Hokkaido (northern Japan) (Igota et al. 2004), 0.03 to 0.4 km^2 in Okuchichibu (eastern Japan) (Takii et al. 2012a), and 0.1 to 0.6 km^2 in Aichi Prefecture (eastern Japan) (Kamata et al. 2020). The size of the core area of sika deer in western Japan was 0.1 to 0.2 km^2, which is relatively small. It is presumed that in Japan as a whole, the core area size is larger at high latitudes.

In western Japan, the use of evergreen coniferous and broad-leaved forests was high, especially in Kyushu; the evergreen broad-leaved forests were used extensively throughout the year. The size of the core area was smaller in Kyushu than Kink, where evergreen broad-leaved forests were intensively used due to the quantity and quality of food resources. However, the home range size may be affected not only by the food resources but also by the body size of the deer, topography, surrounding human activities, and deer density. Since these factors were not evaluated in this analysis, further research is necessary.

14.5.2 Percentage of Seasonal Migrants

The percentage of seasonal migrants was only 38% (17 out of 45 individuals) in Kinki and 10% (7 out of 69 individuals) in Kyushu, compared to 76% in Hokkaido (Igota et al. 2004), 100% (6 of 6 individuals) in Okuchichibu (Takii et al. 2012a), and 65% (15 out of 23 individuals) in Kirigamine (Takii et al. 2012b). Compared to these regions, the proportion of sika deer migrants in western Japan is low. In this survey,

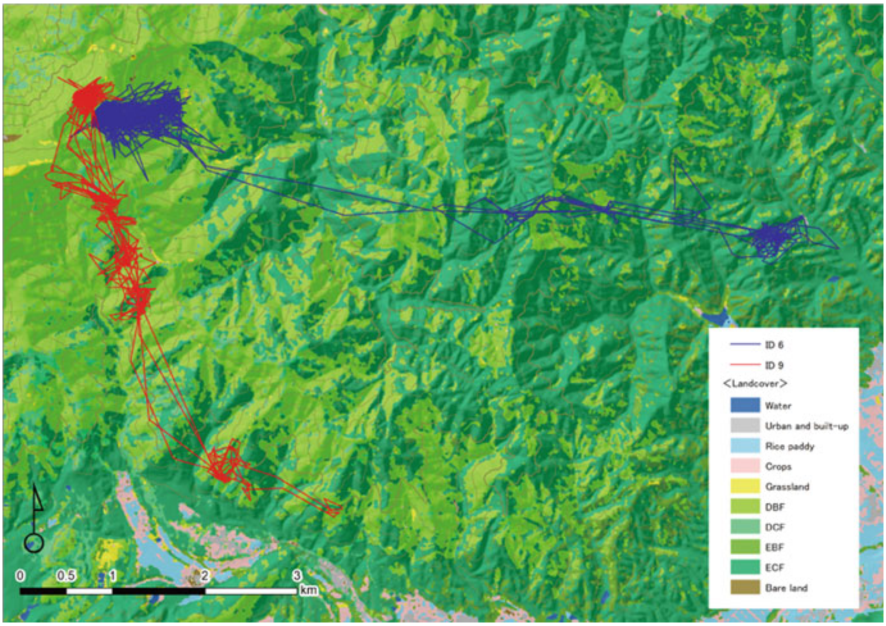

Fig. 14.8 Example of migration routes of two deer (Mt. Ibuki, Shiga Prefecture) ID6 and ID9 are adult females. The land cover is shown as DBF for deciduous broad-leaved forest, DCF for deciduous conifer forest, EBF for evergreen broad-leaved forest, and ECF for evergreen conifer forest

the distance traveled was between 1.9 and 14.3 km for all individuals, compared to 7.2–101.7 km in Hokkaido (Igota et al. 2004), 3.0–40.3 km in Kirigamine (Takii et al. 2012b), and 2.5–31.9 km in Okuchichibu (Takii et al. 2012a). Therefore, the migration distance in western Japan is shorter than those in other regions.

In the Kinki region, the movements of individuals that underwent seasonal migration in winter showed that they did not stay in their winter habitat all the way until spring but that they tried to return to their summer habitat, moved, but then turned back to their winter habitat again (Fig. 14.8). In northern and eastern Japan, deer tend to migrate directly to the wintering ground and remain there until spring. However, the seasonal migrants in western Japan tried to return to their summer home range when the deer was at the wintering ground. From this behavior, we can infer that the winter habitat of the sika deer in western Japan is not a fixed one but rather serves as a temporary shelter from the snow.

14.5.3 Causes of Seasonal Migration

We confirmed that most of the migratory males migrated in winter, while some migrated in autumn and summer. The reason for the individuals migrating in winter can be attributed to the scarcity of food due to snowfall and defoliation, which was clear from the relationship of snow depth and number of days of snow. The breeding season of the sika deer is in the fall, from mid-September to late November (Yamauchi et al. 1997, 1999; Yokoyama et al. 2003), and individuals that migrated in the fall are considered to have migrated for breeding purposes. Another survey in the central mountains of Kyushu (Yabe et al. 2001) also reported that males migrated in the breeding season; therefore, we can confirm that the individuals that migrated in the autumn do so to breed. The vegetation at the summer habitat in Shiga Prefecture was grasslands, and many grazing marks have been confirmed (Wildlife Management Office 2011). Therefore, migration during summer may be due to the search of better-quality food resources.

Meanwhile seasonally migrating females only migrated in winter. Thus, sika deer in western Japan migrated during winter due to scarcity of food resources, while males also migrated to access better forage and breeding areas in summer and autumn.

Considering western Japan as a whole, seasonal migrants often utilized deciduous broad-leaved forests. Particularly, the females in Kinki used deciduous broad-leaved forests from summer to autumn and migrated to evergreen coniferous or evergreen broad-leaved forests in winter. On the other hand, sedentary individuals used deciduous broad-leaved forests in low proportion and evergreen broad-leaved forests and evergreen coniferous forests in high proportion. Fig. 14.9 shows the home range of Mt. Ibuki in Kinki, where many seasonal migrants were present, while the home range of Yakushima, characterized by sedentary individuals, is superimposed on the vegetation map. In Mt. Ibuki, where there were many seasonal migrants, the primary vegetation in the home range was deciduous broad-leaved forests, whereas in Yakushima, where there were many sedentary individuals, the entire home range was covered with evergreen broad-leaved forests, and the home range was significantly small.

The individual that traveled the maximum distance was an adult female in the central mountains of Kyushu. She initiated migration in October, moved southward over 2 days, and stayed there until January of the following year when the collar was recovered (Fig. 14.10). In her summer habitat, the most utilized vegetation was deciduous broad-leaved forests. On the other hand, in her winter habitat, deciduous broad-leaved forests were less used, but evergreen coniferous forests and evergreen broad-leaved forests were mainly used. From these observations, individuals that utilize deciduous broad-leaved forests in summer migrate to evergreen broad-leaved and evergreen coniferous forests as deciduous broad-leaved forests defoliate and snow limits the understory food resources, the forage quantity decrease during the winter. Hence, sika deer migrated to evergreen forests to access food resources. As the snow deepens, evergreen forests can also be used as a shelter, which explains why evergreen forests are used more in winter. On the other hand, individuals inhabiting evergreen forests are more sedentary, because the seasonal changes in the food resources are less.

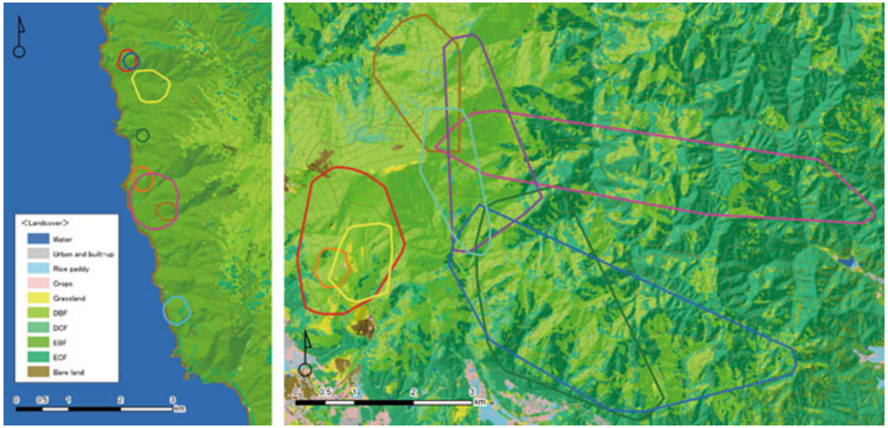

Fig. 14.9 Comparison of the sika deer home range on Yakushima Island, Kagoshima Prefecture, and Mt. Ibuki, Shiga Prefecture. (Left: Yakushima 30°21′N 130°23′E, Right: Mt. Ibuki 35°24′N 136°25′E). The scales of the left and right figures are almost the same

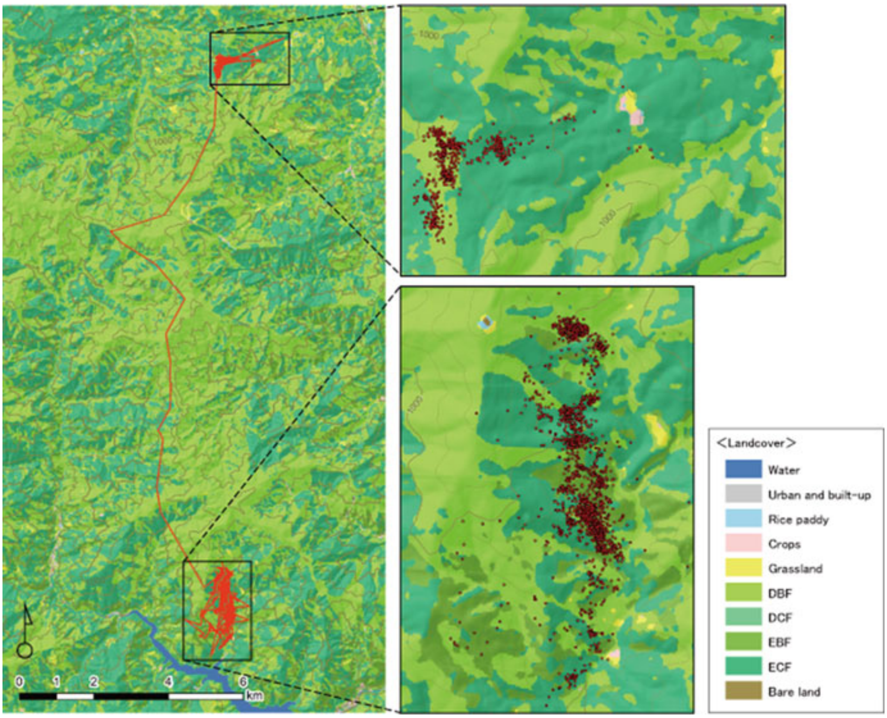

Fig. 14.10 Vegetation used by the seasonal migrants in the summer and winter habitat in Kyushu

14.5.4 Behavioral Characteristics of the Sika Deer in Western Japan

The sika deer in western Japan had a smaller home range and core area than those in northern and eastern regions, and the individuals that migrate seasonally were those from areas with heavy snow. Further, individuals that use deciduous broad-leaved forests as their summer habitat tended to migrate seasonally, while the individuals that used evergreen broad-leaved forests tended to be more sedentary. In this study, although it became clear that the proportion of migratory deer increased in areas with heavy snow, other factors that affect seasonal migration, such as topography, deer density, and human activities, could not be determined.

Japan is a country that stretches long from north to south, with a complex topography and diverse natural environment. Besides, the population density of sika deer and human activities vary from region to region, so their behavioral patterns may differ depending on the anthropogenic impact on the environment. Vegetation and topography in western Japan differ significantly from those in eastern and northern Japan, and deer behavior is also thought to have characteristics unique to western Japan. There are few reports on the behavioral characteristics of Japanese deer in western Japan, and further research is needed.

Acknowledgments We would like to thank the Forestry Agency's Kinki-Chugoku Regional Forest Office and Kyushu Regional Forest Office, the Ministry of the Environment's Chugoku-Shikoku Regional Environment Office, and the prefectures of Shiga, Mie, Tokushima, and Fukuoka for generously providing GPS data.

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Chapter 15
Behavior of Sika Deer in Clear-Cut Areas, Plantations, and Their Surroundings

Takahiro Ohba

Abstract In this chapter, I will report on the home ranges of sika deer in western Shizuoka Prefecture during an entire year when no seasonal migration occurred, based on highly accurate information regarding their location. The study area had well-established forestry industries and included clear-cuts and plantations, as well as their surroundings. The average home range of female sika deer ($n = 7$) in the study area was 73 ha (±30.4 SD), which was fixed and had little overlap with neighboring herds. The overlapping core areas were limited to open environments suitable for sika deer feeding. The home ranges of male adults ($n = 2$) were 73–101 ha and separated by several kilometers, including during the mating period. Sika deer often invaded plantations at night in locations where protective fences had been installed, and the invasions lasted until the fence was repaired. As sika deer did not immediately reinvade the plantation area following the repair, the protective fences were considered to be highly effective. However, they took advantage of some of the entrances created by wild boars who had broken the protective fences. As such, the removal of individuals with home ranges around plantations, in addition to reducing labor costs and ensuring the effective management of protective fences, is important to reduce feeding damage caused by sika deer.

15.1 Introduction

Approximately 60% (25.1 million ha) of Japan's land area is covered by forests, of which approximately 40% (10.35 million ha) are plantations. In these areas, conifers suitable for architectural purposes, such as the fast-growing Japanese cedar (*Cryptomeria japonica*) and the Japanese cypress (*Chamaecyparis obtusa*), have been planted. Many of these plantations were established during the post-World War II period of reconstruction and high economic growth (1950–1970) because of a policy

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T. Ohba (✉)
Forestry and Forest Products Research Center, Shizuoka Prefectural Research Institute of Agriculture and Forestry, Hamamatsu, Shizuoka, Japan
e-mail: takahiro1_ohba@pref.shizuoka.lg.jp

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aimed at expanding forests by cutting down those consisting of natural broad-leaved trees and replacing them with conifer-centered plantations. Currently, most plantations have reached their harvest period after more than 50 years of being planted. However, the presence of sika deer, which damages planted trees, is a major obstacle to the clear-cutting and reforestation of plantations that have reached their harvest season. Forest damage by sika deer became apparent at the beginning of the 1990s, and approximately 20% of forests nationwide have been damaged by these animals in recent years. Approximately 6000–7000 ha of plantations are damaged per year, accounting for approximately 80% of the forest damage caused by wild birds and animals (Ministry of Agriculture, Forestry, and Fisheries [MAFF] 2021).

Sika deer can damage forestry systems by not only causing the slow growth and death of plantation trees and material deterioration due to peeling but also being responsible for the peeling of bark (Iijima and Nagaike 2015) and feeding on standing tree saplings (Akashi et al. 2015; Uno et al. 2019) in natural forests. They also feed on herbaceous plants in the understory of forests (Tamura and Yamane 2017) and semi-natural grasslands (Otsu et al. 2019) resulting in the loss of these species and soil erosion (Furusawa et al. 2003; Chaps. 23 and 27). Additionally, there are concerns related to the decline of potential ecosystem services and ecosystem functions of forests, such as national land conservation and water recharge (Ministry of Agriculture, Forestry, and Fisheries [MAFF] 2021).

To reduce the impact of sika deer on forestry systems and natural forests, it is necessary to continue culling or relocating animals that are in excess of the expected increase of the population in natural conditions and reduce the numbers (Iijima et al. 2013; Chap. 16). In particular, using measures that are based on detailed behavioral information of sika deer as part of forestry operations is important, so that their capture in forestry sites with clear-cuts or plantations is more effective.

This chapter describes a follow-up survey that was conducted to clarify the home ranges of sika deer inhabiting the clear-cut areas, plantations, and their surroundings, as well as the frequency and timing of invasion into plantations to ensure the effectiveness of captures and maintenance of protective fences in the study area. For this survey, a collar including a telemetry transmitter with a global navigation satellite system receiver (hereafter, “GPS collar”) was attached to sika deer.

Prior to the analysis, the accuracy of location data was verified. Even if there were clearly large errors in some points in the obtained location data, in some cases, these could not be excluded by only using an index value indicating the degree of deterioration of positioning accuracy, determined with the number of GPS satellites used to calculate the position, as well as their arrangement. The main cause for this was the multi-path error due to receiving reflected radio waves. With car navigation and portable GPS systems, it is possible to converge multi-path errors by providing continuous locations. However, as the GPS collars used calculation procedures and time limits that only enabled positioning for short periods to reduce battery consumption, it was impossible to correct the error. Therefore, I used another method for extracting highly accurate location points by setting reference values for the elevation error and dilution of precision (DOP) values.

Sika deer's preferred plants flourish in sunny clear-cuts and plantations and attract these animals to such areas, which induces feeding damage to planted trees. As such, the installation of protective fences, as well as their maintenance, is indispensable for the prevention of feeding damage. However, as damage to protective fences themselves and the invasion of wild animals are unpredictable, regular patrolling is required, which involves hiking on steep terrain and high labor costs. Therefore, to save labor costs in patrols, prevent intrusion in a short period of time, and build an animal intrusion detection and reporting system that suppresses damage to planted seedlings, a machine monitoring test was conducted in which a sensor was installed inside the protective fence to detect and report animal invasions.

15.2 Survey Site

The survey site spans across Hamamatsu City, including Tenryu-ku, Sakuma-cho, and Tatsuyama-cho in western Shizuoka prefecture, which is approximately 200 km west of Tokyo. The site includes the Kashi (1059 m altitude) and Shirakura (1027 m altitude) mountains, and a massif where the Tenryu River moves southward to the east (35°N, 137.8°E). Japanese cedar and Japanese cypress plantations represent most of the study area's vegetation, and in recent years, clear-cutting and reforestation have been promoted in the central part of national forests.

The survey site adjoins AMeDAS Sakuma Observatory (latitude 35.1°N, longitude 137.8°E, altitude 150 m), where an average annual rainfall of 2231.8 mm and an average annual temperature of 14.6 °C have been recorded. There is occasional snowfall in winter, but snowfall is not continuous.

15.3 Methods

15.3.1 Extraction of Location Data With Reduced Error

From April to June 2010, GPS collars (Tellus Basic 1D; GPS chip SirfSTARIII, Followit AB, Lindesberg, Örebro, Sweden) were placed in five sites outside the survey area (in Shizuoka Prefecture) with different topography and vegetation conditions: an open area on the roof of a building, a flat Japanese cypress forest on a hill, a Japanese cedar forest on a north-facing slope, a Japanese cypress forest on a north-facing valley, and a Japanese cedar forest on a northeast-facing valley. The collars were fixed with a tripod, and location data was collected for 8–11 consecutive days. Using the obtained location results, I examined a method for extracting data with reduced error.

15.3.2 Home Range

A tranquilizer gun was used to administer xylazine-ketamine to immobilize the animals so that the GPS collars could be placed. I used a syringe with a capacity of 3 ml. The amount of ketamine was 333 mg/3 ml and the amount of xylazine was 57 mg/3 ml, and this composition was the same for all individuals. All procedures involving animal capture were approved by Shizuoka Prefecture under "Wildlife Protection and Proper Hunting Act" (Ministry of the Environment). Ketamine hydrochloride was administered by a trained individual licensed by a drug researcher under the Drug Control Act. Individuals that escaped after being shot with the tranquilizers and later became immobile were searched using infrared thermography (PS-32, Teledyne FLIR LLC, Wilsonville, Oregon, USA). The GPS collars (GLT-03, Circuit Design, Inc., Azumino City, Nagano, Japan) were attached to the immobilized individuals, and their body weights were measured. The GPS collars were fitted to ensure that they would not slide out of their heads, but also not tighten or scratch the animal's neck. In addition, an ear tag (Aussie tag/F2+LM1 With number, Fujihira Industry Co., Ltd., Bunkyo-ku, Tokyo, Japan) widely used in livestock management was attached so that individual identification was possible through direct observation or an automatic camera. After the work was completed, atipamezole hydrochloride was intramuscularly injected to promptly awake the animal.

A total of 21 deer were captured from 2013 to 2019, and the location data were obtained from 15 deer equipped with GPS collars, 3 males and 12 females. The remaining six animals did not recover from anesthesia and died. Separately, four individuals (9I, 10I, 11H, and 12J) were attracted by bait and automatically attached with a GPS collar for short-term tracking (Table 15.2, Fig. 15.1). Generally, location data was collected 12 times per day, every 2 h (every odd hour in Japan time).

The tracking of the individuals was based on the beacon waves emitted from the GPS collars. While checking the direction of the tracked individual using a directional antenna, the individuals were approached to a distance of several hundred meters and downloaded the position data by remote control. The Geographic

Fig. 15.1 Automatically attachment procedure of the GPS collar to the deer (№9I, №10I, №11H, №12J). A GPS collar was attached by triggering its deployment when the deer placed its head in the feeder to feed

Information System (GIS) software (ArcGIS Desktop ver.10 and ver.9 with Extension: Spatial Analyst, ESRI, Redlands, California, USA) was used to extract data with an altitude error of ≤ 30 m and a horizontal dilution of precision (HDOP) of ≤ 4 as high-precision location points. The Home Range Tools for ArcGIS (Center for Northern Forest Ecosystem Research 2007) were used to obtain the home range using the fixed kernel method. Since the home ranges need to be based on several highly accurate location points, the bandwidth was set to 20 m to prevent the home range from being extended to outside the used location points. The 95% fixed kernel was considered the home range area, and the 50% fixed kernel was considered the core area.

15.3.3 Invasion of Sika Deer into New Plantations Enclosed by Protective Fences

A pyroelectric infrared sensor, which is inexpensive and used in automatic photographic cameras, was used to detect the intrusion of sika deer. Five communication terminals (with pyroelectric infrared sensors) were installed in two plantations in the survey area and monitored from November 2020 to May 2021. However, since this sensor also detects temperature changes due to solar radiation, false detections during the daytime occur frequently, especially in areas with open environments, such as plantations. Therefore, monitoring was limited to nighttime to avoid false detections by the sensor, and detections were confirmed by the location information provided by the GPS collars to assess whether there was an intrusion by sika deer.

Among the GPS-tracked individuals, the locations of those that invaded the plantations enclosed by protective fences were analyzed with GIS software. The extracted high-precision location points were overlaid on the polygons created by the protective fences based on the field survey data and base map satellite images, and the location points that were inside the protective fence at the time of intrusion were extracted. The length of the intrusion period and the dates of stay for each day and night were estimated from the date and time details of the obtained location points. In this study, I considered daytime as the time from 9:00 to 15:00 h and nighttime as the time from 21:00 to 3:00 h. All the protective fences installed around the plantations in the study area had the same characteristics (height 1.8 m (bottom 1.0 m contains reinforced fibers), hem 0.6 m, 5 cm mesh polyethylene net).

15.4 Results and Discussion

15.4.1 Extraction of Location Data with Reduced Error

The success rate of positioning in conifer plantations was 96–99% (Table 15.1). However, at the position of the GPS collar installed at a fixed point, an error of up to

Table 15.1 Positioning and extraction results of GPS (Tellus Basic 1D, Followit AB, Sweden) for each condition

Terrain and vegetation	Number of positioning (A)	Positioning success		3D positioning		HDOP≤4		Elevation error ≤ 30 m		Highly accurate positioning points (D) & (E)		Exclusion point	
		(B) (B/A %)	ME (m)	(C) (C/B %)	ME (m)	(D) (D/B %)	ME (m)	(E) (E/B %)	ME (m)	(F) (F/B %)	ME (m)	(G) (G/B)	ME (m)
Flat on a hill, open land	318	318 (100)	10.3	318 (100)	10.3	280 (88)	9.3	288 (91)	8.0	258 (81)	7.2	60 (19)	23.6
Flat on a hill, cypress forest	348	343 (99)	18.5	343 (100)	18.5	297 (87)	13.8	278 (81)	11.4	248 (72)	9.7	95 (28)	41.4
North-facing slope, cedar forest	346	334 (97)	38.5	301 (90)	37.3	213 (64)	33.0	99 (30)	17.5	75 (22)	15.1	259 (78)	45.2
North-facing valley, cypress forest	347	332 (96)	30.5	323 (97)	30.3	239 (72)	25.1	141 (42)	18.3	106 (32)	15.7	226 (68)	37.5
Northeast-facing valley, cedar forest	344	332 (97)	46.4	307 (92)	44.5	233 (70)	37.2	104 (31)	20.1	85 (26)	18.2	247 (74)	56.2

ME mean error

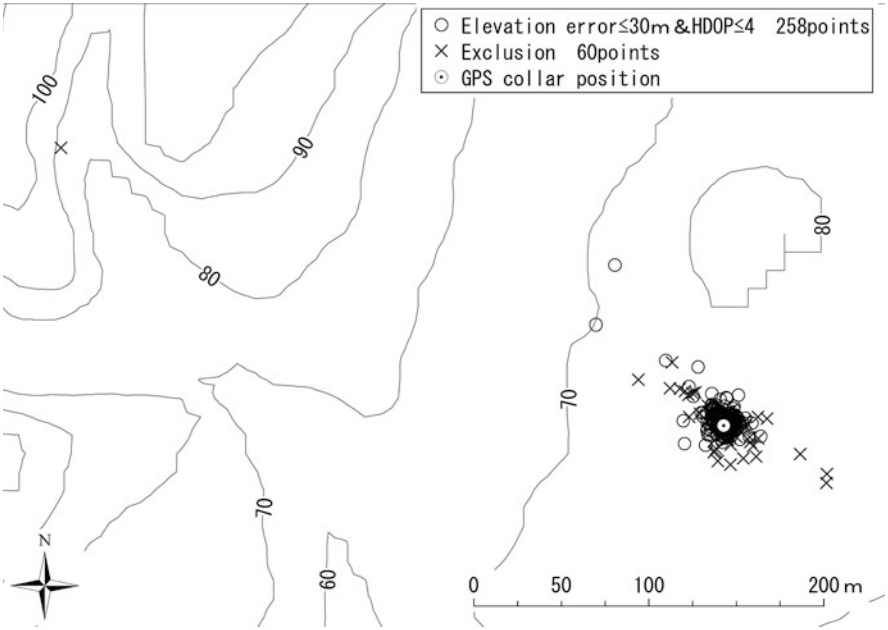


Fig. 15.2 High-precision positioning and exclusion points of GPS (Tellus Basic 1D, Followit, Sweden) for an open area on the roof of a building

several 100 m occurred in the horizontal distance, not only in the conifer plantations but also in the open areas and even for three-dimensional data (Figs. 15.2 and 15.3).

Therefore, using GIS software, most data with large horizontal errors could be excluded by comparing the elevation value obtained by the GPS collars installed at fixed points with the actual elevation value based on the horizontal coordinates of the data using the Fundamental Geospatial Data Digital Elevation Model and only extracting data whose difference was within a 30 m range. The elevation error is considered to be approximately twice the horizontal error (Department of Defense 2020).

Furthermore, if the HDOP value recorded when the location was collected was limited to 4 or less, the amount of data was reduced but the error was smaller. The average error was higher for three-dimensional data, followed by the HDOP, elevation error, and finally elevation error + HDOP (Table 15.1). However, even with this method, not all data containing errors could be excluded (Figs. 15.2 and 15.3). In addition, the proportion of data that could be extracted as high precision location points varied considerably because of differences in topography and vegetation (shielding) (Table 15.1).

Considering that data with large vertical errors tend to also have large horizontal errors, the elevation error of the three-dimensional data was used as the main criterion. Furthermore, by limiting the data to those with DOP below a certain

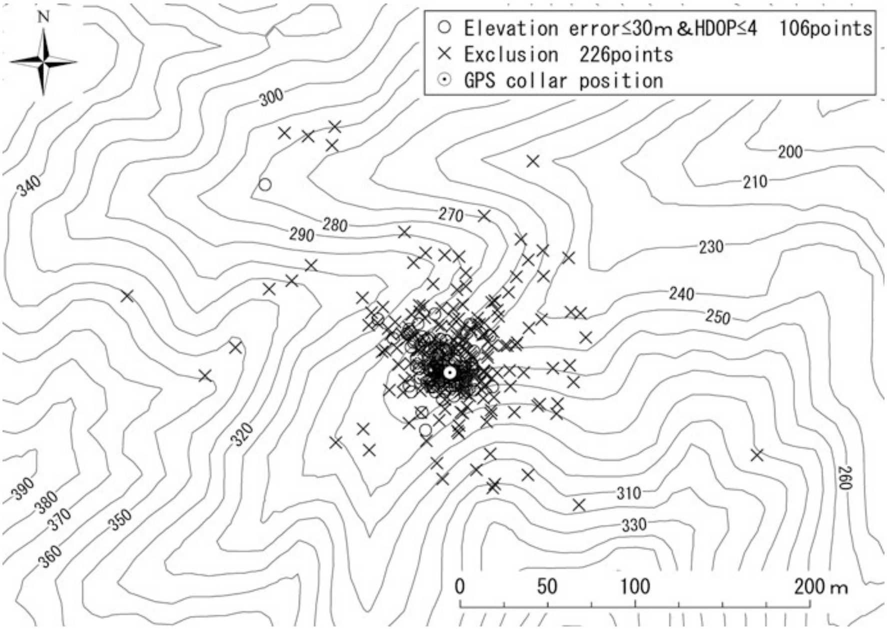


Fig. 15.3 High-precision positioning and exclusion points of GPS (Tellus Basic 1D, Followit, Sweden) in a cedar forest in a northeast-facing valley

level, it was possible to exclude location points with large errors to some extent. The extraction of data used for behavioral analyses from the location data of wild sika deer fitted with GPS collars using this method was considered appropriate. However, it should be noted that the location points, as well as their accuracy, are biased because of the influence of topography and vegetation (shielding) and do not accurately reflect the frequency of use; as such, the environment must be cautiously selected.

15.4.2 Home Range

The home range of seven females (1A, 3C, 5E, 8H, 14K, 16J, and 17L) that could be tracked for 350 days or more was 73.0 ± 30.4 ha (mean ± SD) (Table 15.2); the core area was 10.2 ± 2.6 ha, which was 11–17% of the 95% home range kernel. Only two males (7G and 18 M) could be followed for more than 150 days, including during winter, whose home range was 73.0–101.0 ha and the core area was 7.6–16.4 ha.

When the location data of the tracked individuals was displayed together with GIS software, minimal home range overlap was found, except for the herds of 13K, 14K, and 15K, which were suspected to be infants with respective parents and may have been trapped in the protective fence and captured at the same time; the herds of

Table 15.2 Status of capture and tracking of sika deer and home range size in sugi and cypress plantations in western Shizuoka Prefecture, 2013–2019

ID	Date of capture	Tracking days	Sex and age	Body mass (kg)	Total points	High accuracy positioning ratio (%)	Area of home range kernel (ha)		GPS collar model
							95%	50%	
1A	17 Dec 2013	423	AF	(40)	5058	51.3	54.5	7.3	GLT-01
2B	24 Jan 2014	145	YF	32	1722	63.6	58.5	9.5	GPS PLUS
3C	29 Jul 2014	488	AF	36.5	5864	41.8	50.3	8.5	GLT-01
4D	29 Oct 2014	133	AF	(30)	1598	61.2	22.1	3.7	GLT-01
5E	5 Oct 2016	679	AF	40	8153	46.5	57.8	9.1	GLT-03
6F	19 Oct 2016	165	AF	43	1973	97.6	3.5	0.9	GLT-03
7G	21 Oct 2016	255	AM	62	3128	46.8	73.0	7.6	GLT-01
8H	27 Dec 2016	670	AF	35	8032	55.4	70.5	11.8	GLT-03
9I	22 Feb 2017	16	YM	–	136	51.5	11.2	1.7	GLT-02A
10I	4 Apr 2017	16	J	-	136	66.2	13.6	1.5	GLT-02A
11H	5 Apr 2017	17	J	–	144	42.4	12.1	2.1	GLT-02A
12J	10 Apr 2017	130	J	–	1004	54.3	23.4	4.8	GLT-02A
13K	31 Jan 2018	79	AF	42	913	69.2	49.6	7.5	GPS PLUS
14K	31 Jan 2018	355	YF	26	4126	55.7	80.6	10.7	GPS PLUS
15K	31 Jan 2018	642	J	19	7711	34.9	48.6	4.0	GLT-03
16J	14 Sep 2018	782	AF	48	9370	64.0	59.4	8.7	GLT-03
17L	16 Nov 2018	760	YF	24.5	9107	35.4	137.9	15.0	GLT-03
18M	6 Nov 2018	156	AM	(70)	1864	78.4	101.0	16.4	GLT-03
19N	7 Oct 2019	34	AM	(75)	406	74.4	13.4	1.6	GLT-03
			Average home range for female deer			73.0 ± 30.4		10.2 ± 2.6	

The average home range (±SD) for female deer was calculated from tracking data collected more than 350 days, shown in bold ID ($n = 7$). These are the seven animals for which the average area of the action area was calculated

AF adult female, *YF* yearling female, *AM* adult male, *YM* yearling male, *J* juvenile. Figures in parentheses showed estimated body mass

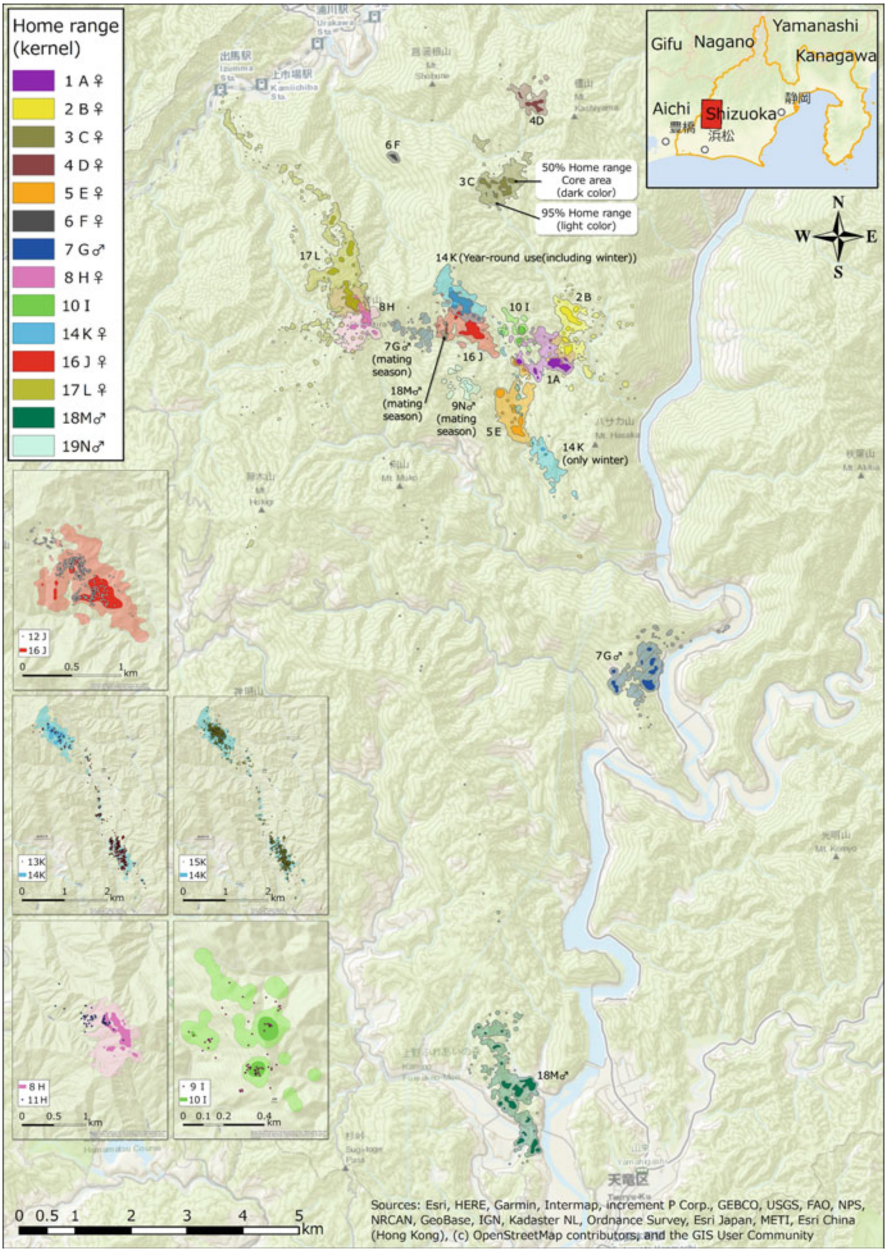
8H and 17L (tracking periods do not overlap), which invaded the same plantation; and the herds of 12J and 16J, 8H and 11H, and 9I and 10I (9I, 10I, 11H, and 12J had GPS collars automatically installed), whose home ranges overlapped considerably (Fig. 15.4). A survey conducted by Iimura (1980) in the Tanzawa Mountains in Kanagawa Prefecture, which is located to the east of Shizuoka Prefecture, showed that field signs such as footprints and fecal content of sika deer were rarely found between some adjacent districts and that individual exchange between districts was uncommon. Additionally, the home range of the six herds based on field sign mapping was 50–80 ha (average 63 ha). The findings of this study showed similar home range sizes, which also did not directly overlap.

In winter, individuals 13K, 14K, and 15K moved their home range to approximately 3 km away from its original location but traveled back and forth between the two, which does not qualify as seasonal migration. Individual 17L made nine round trips to the bottom of the mountain between December and January, which was also not considered seasonal migration, although the reason for these behaviors could not be identified. Despite the occasional deviation, the other females did not move their home ranges to new locations during the tracking period.

The two male adults, 7G and 18M, had stable home ranges after moving away from the survey site in November. Since there was almost no snow cover during winter, it is appropriate to think that the males moved to areas where females inhabit only during the mating season and that they do not move or stay in wintering areas.

As shown in Fig. 15.4, the home range of tracked individuals considerably overlapped with that of the same herd or did not overlap much with other individuals' home range in a different herd. It is likely that the surrounding female herds that are not related avoid each other, and within the same herd the home range is shared and inherited by the blood relatives. As a result, the home ranges of these herds have become more fixed, and there is a possibility that the herds were living separately from each other. In this study, the home range of each sika deer herd was fixed, and there was little overlap between them, even in environments with several clear-cut and reforested areas. Therefore, the removal of sika deer with home ranges around the plantations is expected to reduce the risk of invasion. Notably, the capture and attraction of sika deer to improve the removal efficiency may only work on limited herds whose home ranges include these areas.

The findings of this study showed some overlap between the core areas of different herds, for instance, between those of 1A and 5E in Japanese star anise fields, 8H and 17L in conifer plantations with strong thinning management, and 14K and 16J in hardwood plantations without protective fences. Environments with several understory species are preferred by sika deer as feeding grounds, and if such spots are near the edge of their home range, these may be shared with neighboring herds.



Sources: Esri, HERE, Garmin, Intermap, increment P Corp., GEBCO, USGS, FAO, NPS, NRCAN, GeoBase, IGN, Kadaster NL, Ordnance Survey, Esri Japan, METI, Esri China (Hong Kong), (c) OpenStreetMap contributors, and the GIS User Community

Fig. 15.4 Home range of 19 sika deer tracked in western Shizuoka Prefecture, 2013–2019

15.4.3 Invasion of Sika Deer into Plantations Enclosed by Protective Fences

Of the 19 individuals fitted with GPS collars, 6 (5E, 8H, 14K, 15K, 16J, and 17L) invaded the plantations where the protective fences had been installed (Table 15.2). Table 15.3 lists the characteristics of the plantations and the invasion. Although the invasion length varied, the percentage of days when sika deer were inside the fenced area at night was as high as 88–100%. However, the percentage of days when sika deer were inside the fenced area during the day was 0–87%, which was lower than that at night and had a large variation. As there was no individual that consistently invaded the plantations exclusively during the day, it was considered that limiting the monitoring period to nighttime would not considerably hinder the detection opportunity, as false detections by the pyroelectric infrared sensor are unlikely to occur. Based on this result, a machine monitoring test of the plantations was also conducted using an animal intrusion detection and notification system that combines a pyroelectric infrared sensor and low-power wide-area network communication.

The signal from the communication terminal was transmitted to a base station 7–10 km away via one repeater installed at a high location in the plantation and three

Table 15.3 The period and time of day when deer with GPS collar invade the planting area of the cedar and cypress

ID	Planting area	Planting date	Duration of invasion inside the fence	No. of days (A)	No. of days of invasion inside the fence (B) (B/A%)	Nighttime invasion (C) (C/B %)	Daytime invasion (D) (D/B %)
5E	Area A	May 2016	Aug 5–Dec 22, 2017	139	121 (87)	118 (98)	2 (2)
8H	Area B	Mar 2017	May 31–Jul 17, 2018	47	43 (91)	43 (100)	27 (63)
14K	Area C	May 2015	Oct 21–Oct 28, 2018	8	8 (100)	8 (100)	1 (13)
15K	Area C	May 2015	Oct 21–Oct 28, 2018	8	8 (100)	7 (88)	0 (0)
15K	Area C	May 2015	Jul 1–Oct 30, 2019[a]	121[a]	120 (99)	114 (95)	104 (87)
16J	Area D	Jun 2015	Nov 7, 2018–Apr 12, 2019	157	126 (80)	124 (98)	0 (0)
16J	Area D	Jun 2015	Dec 5, 2019–Mar 4, 2020	91	89 (98)	89 (100)	4 (4)
17L	Area B	Mar 2017	Mar 30–May 11, 2020	43	40 (93)	40 (100)	1 (3)

[a] Tracking period

repeaters installed in two transmission towers, where information was sent from the base station to the cloud server via a mobile phone line. Repeaters and communication terminals consume less power and run on batteries for long periods. Although the test in which made humans acted as invading animals was successful, verification of these results was attempted with an automatic camera, but there was no invasion of sika deer during that period.

It is likely that sika deer that invaded plantations often left those areas during the day. If the invasion of the sika deer was confirmed, it is possible to confine the individual inside the fence by closing the entrance at night. However, as occurred when individuals 8H and 15K invaded the plantations for a second time, sika deer sometimes remain there during the daytime; as such, when repairing the fence if it is broken, it is also necessary to ensure that no invading individuals are trapped.

Additionally, reinvasion did not occur immediately after repairing the fence with six animals. Based on this, it was considered that the avoidance effect of the protective fence on the sika deer was high (the sika deer's willingness to break through the protective fence was low). However, the holes in the fence's net with reinforced fibers were made by wild boars (*Sus scrofa*), which sika deer also used (Fig. 15.5). The wild boars' ability to cut the net is likely to be greater than that of sika deer, because of their fangs that can break through the protective fence causing the hem to flip up at the tip of their nose. Consequently, the effectiveness of the protective fence to prevent plantation damage from sika deer feeding may depend on the behavior of wild boars.

In conclusion, the removal of individuals with home ranges around plantations, in addition to reducing labor costs and ensuring the effective management of protective fences, is important to reduce feeding damage caused by sika deer in clear-cut areas and plantations.

Fig. 15.5 №16J exiting from the intrusion point (left), wild boar entering the planting area from the same point (right)

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Part III

Impact on Vegetation and Bottom-Up Effect on Sika Deer

Chapter 16
Effects of High Densities of Sika Deer on Vegetation and the Restoration Goal: Lessons from Deer-Vegetation Interactions on Nakanoshima Island, Lake Toya

Masami Miyaki and Koichi Kaji

Abstract We investigated deer-vegetation interactions for an introduced sika deer population on Nakanoshima Island in Lake Toya, Hokkaido, Japan. This population showed repeated irruptions, shifting alternative food resources, and was sustained at a high density (>20 km^2) for over 30 years. The most severe effect of selective foraging by deer occurred during the initial irruption in the early 1980s. Highly palatable species for herbivores, namely, tree species and dwarf bamboos, were eliminated by deer, resulting in browsing lines and expanding populations of unpalatable plants. Death due to bark stripping decreased tree density and promoted the growth of the remaining trees, which resulted in the same effect as the thinning performed in forest operations. Additionally, forest stands further reduced their density as the stand volume increased and the forest layer closed. The combination of windthrows due to typhoons and overbrowsing by deer might also contribute to the rapid decline of forests. Therefore, it is essential to eliminate deer or reduce the density of their population for approximately 30 years to restore deteriorated forest ecosystems. Consequently, for a holistic approach to forest and ecosystem management, hunting as resource management tool and culling for ecosystem management should be synergistically combined under adaptive management.

16.1 Introduction

The damage to agriculture and forestry due to the increase in the number of sika deer has been remarkable in the eastern part of Hokkaido since the beginning of the 1990s and reached its peak in the mid-1990s (Chap. 32). The population had spread to the western part of Hokkaido by the 1990s (Kaji et al. 2000) and subsequently increased

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Masami Miyaki was deceased at the time of publication.

K. Kaji (✉)
Tokyo University of Agriculture and Technology (Retied), Fuchu, Japan
e-mail: kkaji@cc.tuat.ac.jp

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in number. The irruption of sika deer populations also damaged natural vegetation in the Akan-Mashu National Park (NP), Shiretoko NP, and the Kushiro-Shitsugen (mire) NP on Hokkaido (Chap. 32).

Before these events, an introduced sika deer population has been interrupting and severely damaging a forest on Nakanoshima Island in Lake Toya, Hokkaido, since 1980, leading to the monitoring of deer-vegetation interactions (Kaji et al. 2009; Miyaki and Kaji 2009). It was observed that the sika deer population showed repeated irruption with changing staple foods, which caused significant changes in the area's flora (Sukeno and Miyaki 2007). After the initial population crash in 1984, the forest on the island was maintained for a relatively long period (>30 years), even at high deer densities (>20 deer/km^2); however, forest structure became disturbed due to the combined factors of windthrow from a typhoon and overbrowsing by deer. The windthrow caused by typhoons is the most significant disturbance, causing catastrophic damage to forest ecosystems in Japan (Kamimura and Shiraishi 2007; Yamanoi et al. 2015). In addition, because the high-density sika deer population is distributed elsewhere in Japan (Ministry of Environment 2015), the combination of two disturbance factors in forests is likely to occur in various places of the region. Although the combined effect of deer browsing and canopy gap formation on vegetation has been examined (Suzuki and Ito 2014; Itô 2016), there was little knowledge about the combined effect of typhoons and deer browsing on vegetation. Therefore, a holistic approach to deer and forestry management is urgently needed. The management of deer and forests will become more complicated as wildlife biologists and national park managers adopt an ecosystem-based approach to management. Lessons from long-term monitoring of deer-vegetation interactions on Nakanoshima Island, Lake Toya, will help to conceptualize a holistic approach to deer and forest management.

16.2 Study Area

We conducted the research on the Nakanoshima Islands in Toya Lake, Hokkaido, Japan (140°51′ E, 42°36′N). The group of islands is composed of one major island, Nakanoshima (497.8 ha), and two relatively small islands, Benten-Kannonjima Island (23.0 ha) and Manjujima Island (3.8 ha). These three islands, which have a total area of 5.2 km^2, are centrally located in the caldera lake and lie 3 km away from the surrounding mainland. The elevation of the islands ranges from 80 m to 450 m above sea level, and there are no predators or hunting on the island. The climate on Nakanoshima Island is described as having cool summers and mild winters. The maximum snow depth is approximately 50 cm, and the mean annual precipitation is 1112 mm. The highest temperature was 24.7 °C in August, and the lowest temperature was −5.6 °C in February, according to the Toya Limnological Station for Environmental Biology at Hokkaido University, which is 4 km west of the island (Miyaki and Kaji 2009). Deciduous broad-leaved forests dominate 87.1% of the islands. Forest gaps in deciduous forests, artificial conifer forests, and grasslands are

Fig. 16.1 The major understory of deciduous broad-leaved forests on Nakanoshima Island in the early stage of initial irruption had no apparent impact from deer feeding. (**a**) *Sasa senanensis* (dwarf bamboo), (**b**) *Cephalotaxus harringtonia* var. *nana* (plum yew), (**c**) ferns, and (**d**) *Equisetum hyemale* (scouring rush). (**a**) was taken in 1979, (**b**) in 1980, and (**c**) and (**d**) in 1981

4.7%, 6.3%, and 1.6% of the total area of the islands, respectively. The major canopy species in the deciduous forests are *Quercus crispula* (mizunara (white) oak), *Kalopanax pictus* (castor aralia), *Magnolia obovata* (magnolia), *Acer mono* var. *glabrum* (painted maple), *Maackia amurensis* var. *buergeri* (maackia), *Tilia japonica* (linden), and *Ostrya japonica* (hop hornbeam).

After the introduction of three sika deer on the island between 1957 and 1965, the population increased to 299 deer (58 deer/km^2) in the autumn of 1983, and decreased to 137 deer (26 deer/km^2) due to both natural mortality ($n = 67$) and removal ($n = 95$) from the island (Kaji et al. 2009). Following the initial irruption, the population density remained high, ranging from 23 to 84 deer/km^2 from 1984 to 2012 (Ueno et al. 2018).

By 1980, the forest floor was dominated by *Sasa senanensis* (dwarf bamboo) (Figs. 16.1a and 16.2a), ferns (Fig. 16.1b), *Cephalotaxus harringtonia* var. *nana* (plum yew) (Fig. 16.1c), and *Equisetum hyemale* (scouring rush) (Fig. 16.1d). However, high densities of deer eliminated the populations of dwarf bamboo by 1983 (Fig. 16.2b, c) and scouring rush around 1984; thereafter, these plants remained only in the fenced exclosure (Fig. 16.3). The forest floor was dominated by unpalatable species for sika deer such as plum yew, *Senecio cannabifolius* (Aleutian ragwort), *Chloranthus japonicus* (chloranthus), *Pachysandra terminalis*

Fig. 16.2 (**a**) *Sasa senanensis* (dwarf bamboo) was still abundant in 1981; however, (**b**) it was heavily browsed in the wintering yard in 1982 and (**c**) was eliminated by 1983 excluding those within the exclosure fence. (**a**) was taken in 1981, (**b**) in 1982, and (**c**) in 1988

(spurge) (Fig. 16.4), *Daphne kamtschatica* (daphne), *Arisaema peninsulae* (Japanese cobra lily), and *Paeonia japonica* (peony) (Miyaki and Kaji 2004).

16.3 Changes in Flora

The most severe effect of selective foraging by deer on vascular plants occurred during the initial irruption of the early 1980s. Flora on the island changed in the following order (Kaji et al. 1991): (1) the area formerly occupied by taller plants was

Fig. 16.3 *Equisetum hyemale* (scouring rush) was eliminated during the initial irruption, excluding those within the enclosure fence in 1989

replaced by short grasses or unpalatable plants; (2) the elimination of lianas, ferns, and dwarf bamboo occurred; (3) browsing lines became visible; (4) bark stripping damage increased on trees with thinner stems (<15 cm diameter at breast height) and extended to palatable trees with thicker stems; and (5) the population of unpalatable plants expanded.

Concerning vascular plants confirmed on the island, there were 460 species in 1977 when deer density was low (Ozaki 1997), but the plant species declined to only 121 species (26.3%) in 2004 due to long-term browsing (Sukeno and Miyaki 2007). A significant decrease between 1977 and 2004 was found in herbaceous plants from 359 to 67 species (18.7%) and shrub species from 40 to 14 species (35%) that were at the forageable height by deer. Moreover, regarding tree species, the members of the elm genus (*Ulmus laciniata* and *U. davidiana*) disappeared.

Fig. 16.4 *Pachysandra terminalis* (spurge) expanded and dominated in large gaps in the deciduous broad-leaved forest in 2011

16.4 Changes in Grassland

In 1981, the grassland in the central part of the island consisted of forbs, grasses (>30 cm in height), and tall plants (>100 cm) such as *Miscanthus sinensis* (Japanese pampas grass), *Angelica ursina* (Angelica), and Aleutian ragwort, which did not exhibit the apparent effects of grazing (Kaji et al. 1988; Fig. 16.5a). From the increasing grazing impact by deer (Fig. 16.5b), all tall plants became eliminated except Aleutian ragwort (Fig. 16.5c, d). After the initial crash in the winter of 1983–1984, Aleutian ragwort, *Pachysandra terminalis* (Japanese spurge), *Taraxacum officinale* (dandelion), and *Oxalis acetosella* (wood sorrel) increased in numbers (Kaji et al. 1988; Fig. 16.5d).

We monitored long-term vegetation changes in the grassland (1984–2013) using five 2 × 2 m plots set in September 1984 (Fig. 16.6). The palatable species (Gramineae, dandelion, *Trifolium repens* (Dutch clover)) disappeared in 1990 (Fig. 16.6a), while unpalatable plants (spurge) continued to expand (Fig. 16.6b). Notably, Aleutian ragwort increased as an unpalatable plant by 1990 but then decreased due to deer grazing. Furthermore, plum yew and woody vegetation located in one plot located at the forest edge of the grassland, which had also increased as an unpalatable plant, was eaten and eliminated by 2002 (Fig. 16.6c).

Fig. 16.5 Successive vegetation changes in the grassland at the central part of Nakanoshima Island during the initial irruption (1980–1984). The vegetation consisted of (**a**) tall plants (>100 cm) such as *Miscanthus sinensis* (Japanese pampas grass), *Angelica ursina* (Angelica), and *Senecio cannabifolius* (Aleutian ragwort) without the apparent effect of grazing. (**b**) Half of the total deer population concentrated on the grassland for feeding. (**c**) All tall plants were eliminated by deer and (**d**) expanded unpalatable plants such as Aleutian ragwort. (**a**) was taken in 1980, (**b**) in 1983, (**c**) in 1982, and (**d**) in 1984

16.5 Changes in Forest Stands

16.5.1 Understory Vegetation

We assessed understory vegetation (up to 2 m in height) in forest stands on the main island and two adjacent islands, using the deer browse survey method proposed by Aldous (1944), between 1981 and 1983 (Kaji and Yajima 1992). Circular plots (4 m radius in 1981, $n = 68$; 3 m radius in 1982 and 1983, $n = 48$) were set up at intervals of 30 m along randomly selected lines. The most dominant understory populations were the dwarf bamboos and plum yew on the main island and on Benten-Kannonjima Island (Table 16.1).

In 1981, there were three species of dwarf bamboo on the islands. *Sasa senanensis* and a small amount of *S. kurilensis* had covered a quarter of Nakanoshima Island (Kaji et al. 1988; Fig. 16.7). *Sasa senanensis* remained scarce on Benten-Kannonjima Island because of heavy grazing by a pair of sheep, while *S. nipponica* was distributed on Manjujima Island without browsing in 1981. *Sasa senanensis* occurred in 85% of the plots ($n = 60$) with an average coverage of 56% on the main island in 1983; however, it was eliminated by 1983 because of deer browsing. In addition, dwarf bamboos on Benten-Kannonjima Island and Manjujima Island were eliminated by deer in 1983 and 1984, respectively, and the first crash in

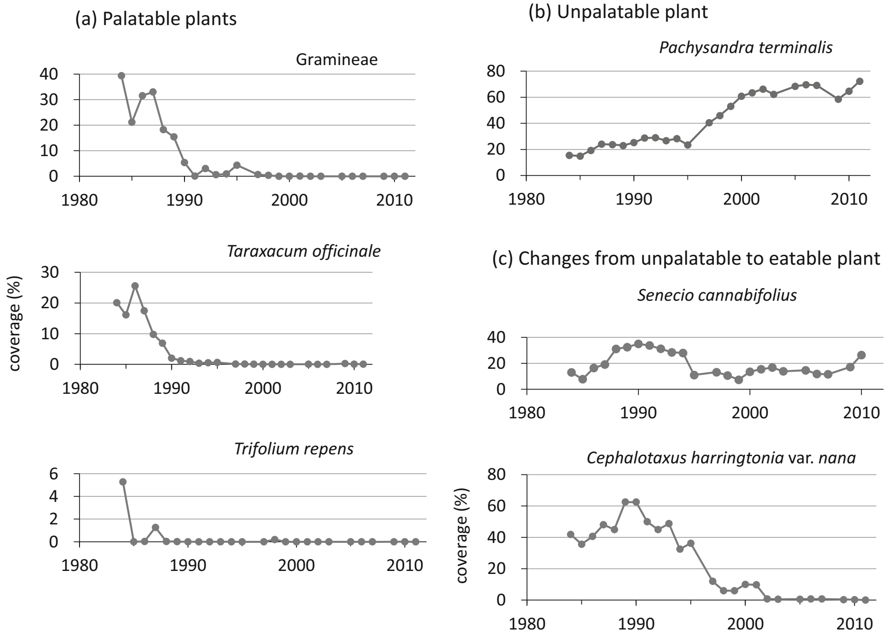

Fig. 16.6 Long-term vegetation changes in the grassland at the central part of Nakanoshima Island, 1984–2011. Under heavy grazing (**a**) palatable plants (Gramineae, *Taraxacum officinale*, and *Trifolium repens*) decreased, while (**b**) unpalatable plants (*Pachysandra terminalis*) continued to increase. (**c**) *Senecio cannabifolius* and *Cephalotaxus harringtonia* var. *nana* increased after the initial irruption; however, while they both decreased from around 1990, the latter was eliminated by the early 2000s

Table 16.1 Average browse cover (%) for understory vegetation on the Nakanoshima Islands in Toya Lake, Hokkaido, Japan, in 1981–1983 (Kaji and Yajima 1992)

	Nakanoshima Is.			Benten-Kannonjima Is.			Manjujima Is.	
Items	1981	1982	1983	1981	1982	1983	1982	1983
No. plot	60	34	34	8	7	7	7	7
Browse cover	20	16	14	8	2	1	36	10
Sasa senanensis	56 (85)	33 (50)	0 (0)	23 (100)	23 (100)	3 (57)	–	–
Sasa kurilensis	11 (18.3)	25 (35)	0 (0)	–	–	–	–	–
Sasa nipponica	–	–	–	–	–	–	58 (100)	39 (100)
Cephalotaxus harringtonia var. *nana*	n.d.	44 (97)	54 (100)	n.d.	22 (100)	39 (100)	–	–
Equisetum hyemale	n.d.	18 (35)	5 (32)	n.d	75 (100)	59 (100)	–	–

Figure in parentheses shows the percent of plots present

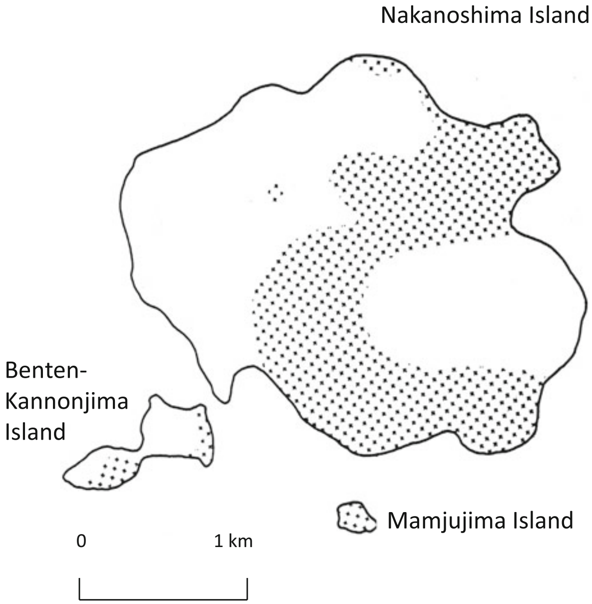

Fig. 16.7 Distribution of dwarf bamboo on Nakanoshima Island, Benten-Kannonjima Island, and Manjujima Island in 1981 (Kaji 1986)

Table 16.2 Relationship between relative deer density (RDD) and its effects on vegetation on Nakanoshima Island and Cape Shiretoko in Hokkaido, Japan (Kaji et al. 2010)

RDD	Nakanoshima Island	Cape Shiretoko
Low <20% *K*	No data	Impacts are minor to moderate: Small trees disappeared and browsing line appeared
Low-moderate 20–39%*K*	No data	No data
Moderate-high 40–59%*K*	Impacts are obvious: Saplings disappeared, dwarf bamboo and small tree populations declined on wintering grounds	Impacts are obvious: Dwarf bamboo and tall plants disappeared; unpalatable plants increased in number
High ≥60%*K*	Great impacts: Tall grass disappeared, browsing line appeared, dwarf bamboos disappeared, large trees were stripped of their bark, and unpalatable plants increased in number	Great impacts: Large oak trees were stripped of their bark

Classification of RDD (low, moderate, and high) was based on the work done by de Calesta and Stout (1997)

1984 coincided with the elimination of dwarf bamboo (Kaji et al. 1988). Plum yew was dominant in almost all plots on the main island and Benten-Kannonjima Island, and its coverage slightly increased from 1982 to 1983 (Table 16.2); however, it was eliminated by 2004 because sika deer had used it for winter food.

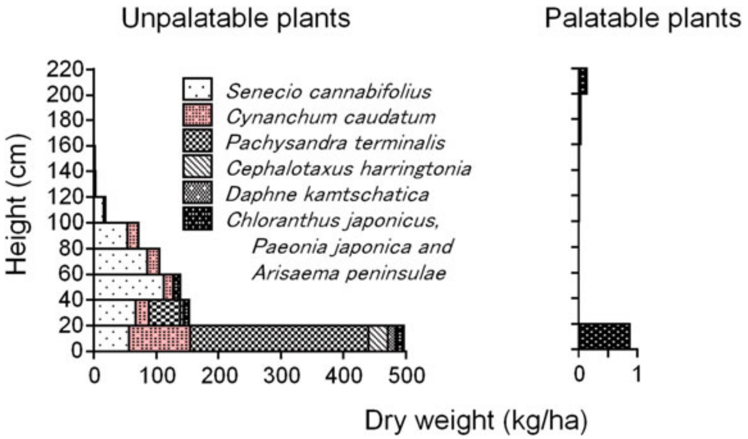

Fig. 16.8 Biomass of forest floor plants and deciduous leaves in deciduous forests on Nakanoshima Island, Toya Lake, Hokkaido, Japan, in July 1994 (Miyaki and Kaji 2004)

16.5.2 *Understory Biomass*

In deciduous broad-leaved forests on the island, understory biomass of palatable plants at heights <20 cm (0.872 kg/ha), and deciduous leaves at height ≥40 cm (0.225 kg/ha), decreased to 0.1% of biomass within the browsing category (up to 2.2 m in height) in 1994 (Miyaki and Kaji 2004) (Fig. 16.8). However, unpalatable plants such as Aleutian ragwort, chloranthus, spurge, and plum yew occupied 9.9% (1018.3 kg) of biomass on the forest floor (Miyaki and Kaji 2004) (Fig. 16.8). The deciduous broad-leaved forest floor is a plagioclimax community in which dominance rests with either unpalatable plants such as the Aleutian ragwort or bare ground where the soil has been eroded and the roots have risen.

The high foraging pressure of the sika deer also had a significant impact on forest structure as trees with a breast height of 5 cm or less were rarely seen on the island. Furthermore, the layer from the ground to heights of 2.2 m within the browsing category in the deciduous forest had few branches and leaves on the trees, and a clear browsing line was formed (Miyaki and Kaji 2004).

16.6 Dynamics of Forest Stands

We predicted changes in forest structure with increasing deer density and analyzed the effect of deer on forest stands using a yield density diagram. In doing so, we compared four pairs of exclosure with each pair comprising a fenced experimental exclosure (10 × 20 m) and an unfenced control (10 × 10 m) (Miyaki and Kaji 2009). *Y-N* curves express the relationship between the cumulative summation (*Y*) of individual tree volume from a maximum-sized tree to one of a certain given volume, and the number (*N*) of these trees on a double logarithmic scale, which is used as a yield-density diagram of forest stands (Kikuzawa 1982, 1999).

16.6.1 Predictions for Forest Changes

Stage 1 While deer density increases at the early stage, the forest loses small trees because of browsing and bark stripping of young trees.

Stage 2 As deer density increases, bark stripping extends to medium- and large-sized trees.

Stage 3 Bark stripping decreases because fewer palatable trees are available, even though deer density is still high. The remaining trees grow in good condition and the total stand volume increases.

Stage 4 After the crown layer is closed, the number of trees will decrease because of the competition among trees; however, the stand volume will still increase.

Stage 5 Lastly, both the number of trees and the stand volume will decrease. The areas of forest gaps will expand during this stage.

The occurrences of bark stripping were concentrated in the initial irruption in the early 1980s and restricted to only six species, *Hydrangea petiolaris* (climbing hydrangea), *Ulmus davidiana* (Japanese elm), *Picrasma quassioides* (Indian quassiawood), *Cornus controversa* (giant dogwood), *Styrax obassia* (fragrant snowbell), and *Taxus cuspidata* (Japanese yew), which comprised 67.9% of the trees killed by bark stripping. Nevertheless, of these species, the number of trees was only 17.5% of the total number of trees (34 species) (Miyaki and Kaji 2009), which corresponded to the description predicted in stage 2. The trees killed by bark stripping were scattered throughout the stand, resulting in small gaps and after the elimination of these palatable trees, bark stripping almost ceased completely.

Seedlings in the unfenced controls were almost totally composed of individuals that were ≤ 10 cm in height 6 years after establishing the plots. Meanwhile in the exclosure plots, the number of seedlings decreased about 8 years after exclosure establishment or after about 8 to 10 years of gap formation due to bark stripping (Miyaki and Kaji 2009; Fig. 16.9).

In the unfenced controls, the recruitment of saplings to tree classes greater than 1.3 m in height was not observed. Meanwhile in the exclosure plots, after the exclosures were set up in 1984, the number of saplings (DBH < 5 cm) increased in Exclosure-A and Exclosure-B. However, there were few or no recruits from sapling to small tree classes in Exclosure-C and Exclosure-D throughout the study period (Miyaki and Kaji 2009; Fig. 16.10). The disappearance of small gaps might cause a decrease in seedling numbers in the exclosure through the closing of the canopy and the consequent darkening of the forest floor. Moreover, in the 1994 and

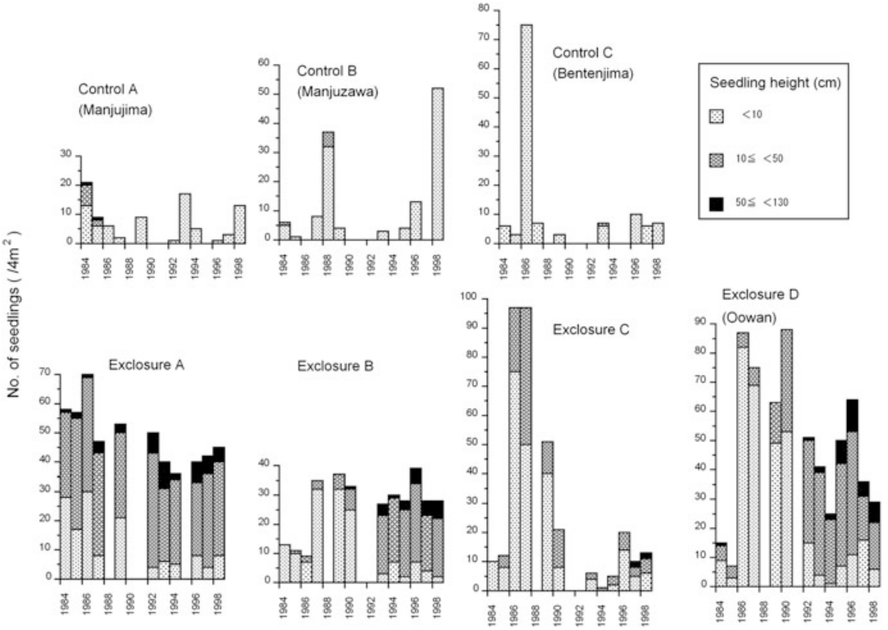

Fig. 16.9 Changes in the number of seedlings in the unfenced control plots and fenced exclosures (Miyaki and Kaji 2009)

2000 surveys, dead trees with a DBH ≥ 5 cm were also found. Therefore, even in the exclosure plots, it is probable that there was no recruitment from saplings due to the closing canopy, but competition among individual trees occurred.

By observing the changes in the *Y-N* curve over time in each survey area, it is possible to grasp the changes in the stand volume, as well as the number and the size distribution of individuals through the competitive relationship between forest structure and dynamics (Fig. 16.11). Stage 1 and stage 2 of the *Y-N* curve would have already passed when the exclosures were established in 1984, while severe browsing and bark stripping occurred in the initial irruption of the early 1980s. Based on movements of *Y-N* curves from 1984 to 2000 each exclosure and control plots (A, B, C, D), we diagnosed the impacts of deer on forest structures that Exclosure-A as stage 2 to stage 3; Control-A as stage 2; Exclosure-B and C, and Control-B and C as stage 3; and Exclosure-D as being in stage 3 or stage 4 (Miyaki and Kaji 2009). These results suggested that the forest of Nakanoshima Island has recovered in stage 4; however, not yet reached stage 5, which take as long as the tree life span (Miyaki and Kaji 2009).

The relationship between relative photosynthetically active radiation (PAR) in forests in 1999 and the growth rate of stand volume/year (1994–1999) revealed that the growth rate tended to be high in stands with brightly lit forest floors. However, the PAR of the forest floor was dark at 1.0% to 3.9%, except in one exclosure that measured 9.0%. Furthermore, there was no difference in the brightness and growth

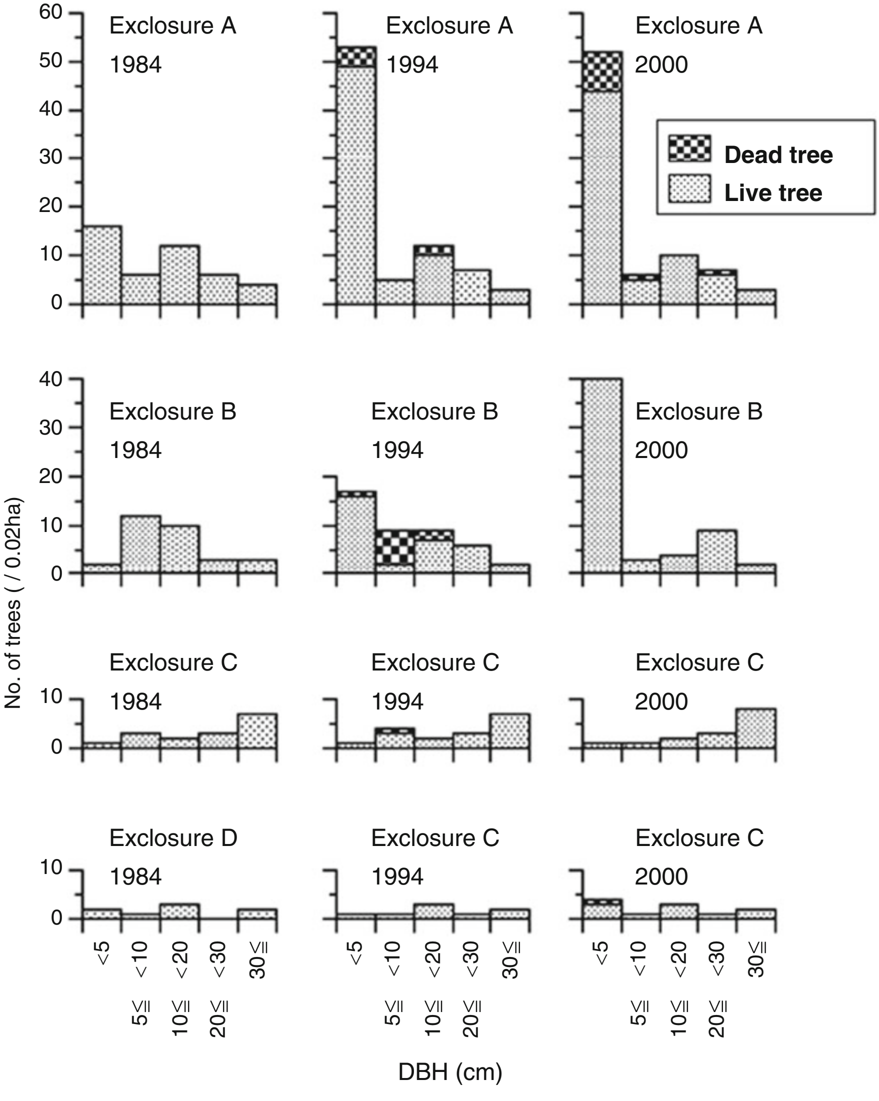

Fig. 16.10 Changes in the number of trees in the exclosures in 1984, 1994, and 2000 (Miyaki and Kaji 2009)

rate of the forest floor between the control and exclosure plots (Miyaki and Kaji 2009). In the control plot, the upper trees grew and the forest floor became dark, as in the exclosure plot. This indicates that the conditions for the enormous growth of saplings were not as expected, even in the absence of deer as already suggested in a previous study (Suzuki and Ito 2014).

Long-term monitoring revealed steady stand growth in both the exclosure and the control plots. Stage 4 has a similar description to that of stage 3 as a stand in which

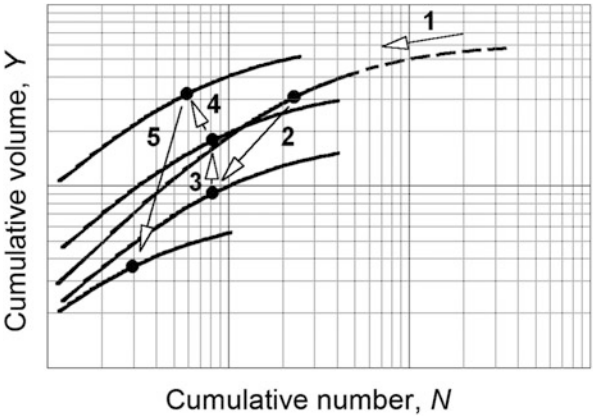

Fig. 16.11 Prediction about the change of forest structure with high deer density. Five stages are shown by the movements of the Y-N curves and B-points (•). Arrows indicate the order over time and numerals show the stages as follows (Miyaki and Kaji 2009). Stage 1: Loss of small-sized trees. Stage 2: Death caused by bark-stripping of medium- and large-sized trees. Stage 3: Growth of individual trees and increase of stand volume. Stage 4: Decrease of number of trees and growth of stand volume. Stage 5: Decrease of number of trees and stand volume

growth reaches full density and subsequently reduces its density, by natural thinning, with increasing stand volume and a closed forest layer (Miyaki and Kaji 2009). We can conclude that the growth of the stand on the island recovered in stage 4.

In general, bark stripping reduces tree density and promotes an increase in the canopy gap rate (Akashi and Nakashizuka 1999). The time scale of forest dynamics is much longer than that of the deer population, and many forests can survive for several decades without the recruitment of seedlings in stage 4. Thus, if the target of forest management is to maintain a given forest structure in the short-term period of 10 to 30 years, a high deer population density could be sustained (Miyaki and Kaji 2009).

16.7 Disturbance from Typhoons and Overbrowsing

We could not confirm stage 5 in the forests on the island, and it may take as long as the tree life span to reach stage 5 under long-lasting high-density (>20 km^2) deer populations (Miyaki and Kaji 2009). However, the combination of two ecological disturbances, windthrows due to typhoons and overbrowsing by deer, might contribute to the rapid decline of forests, which leads to stage 5. On Nakanoshima Island, two large-scale windthrows due to typhoons in 1954 (Typhoon Toyamaru) and 2004 (Typhoon No. 18) caused windthrow.

Tree-ring chronologies of disks from fallen trees ($n = 65$) in 2004 were analyzed to investigate the influence of the windfall in 1954 and bark stripping of sika deer

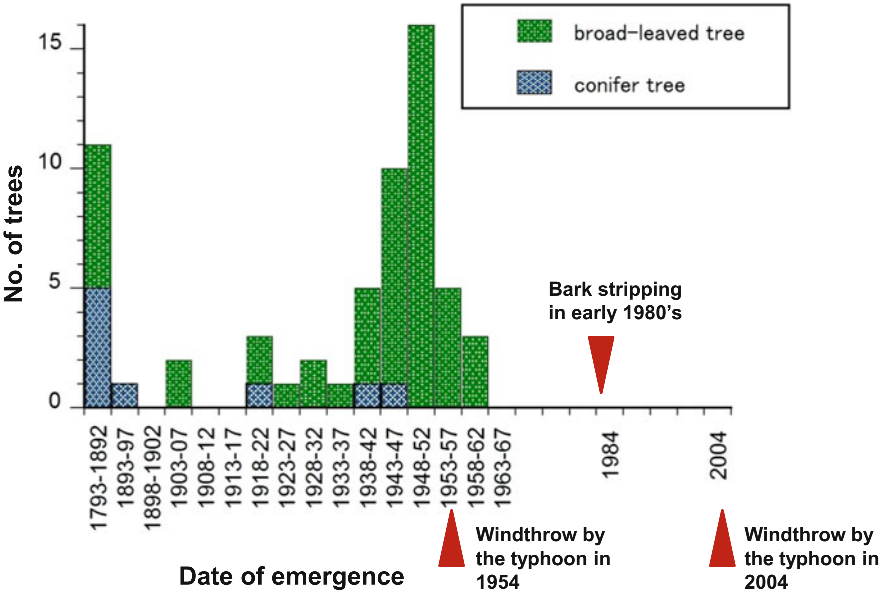

Fig. 16.12 Frequency distribution of emergence date and incidences of windthrow by typhoons in 1954 and 2004. Data showing three ecological disturbances were also presented. After the windfall in 1954, small-diameter trees disappeared in the 1980s (Miyaki 2011)

around 1984 when the deer population crash occurred (Miyaki 2011). The sample trees were divided into groups before 1897 and a group with a peak in 1942–1952 (Fig. 16.12). The youngest tree emerged in 1960. On the island, the sapling population at the time of windthrow in 1954 was intensively renewed. Thus, windfall promoted sapling renewal and played an essential role in forest regeneration. However, after its emergence in 1960, renewal trees were absent, which might have disappeared due to browsing and bark stripping by sika deer.

The relative growth rate of stem volume from fallen trees in each of four decades (1954–1993) on the island reached its peak in the decade after the initial population crash (1984–1993), especially among trees with 10 cm DBH in 1984. This suggests a thinning effect caused by bark stripping (Namikawa et al. 2018). Further, the ring width index (RWI), shown by the ratio of the average annual ring width for each year to the total average annual ring width from sampled windthrows, demonstrated a significant increase both after the windfall in 1954 and after the first crash of sika deer as well as the occurrence of bark stripping in 1984 (Fig. 16.13). The steady growth of trees after a disturbance lasted longer after windthrows in 1954 than after bark stripping in 1984. When the effect of deer on forests was small, as in 1954, the windthrow site became the stage of regeneration. However, under high deer population density, the windthrow sites became occupied by the Aleutian ragwort community, which caused the suppression of tree regeneration. In habitats with

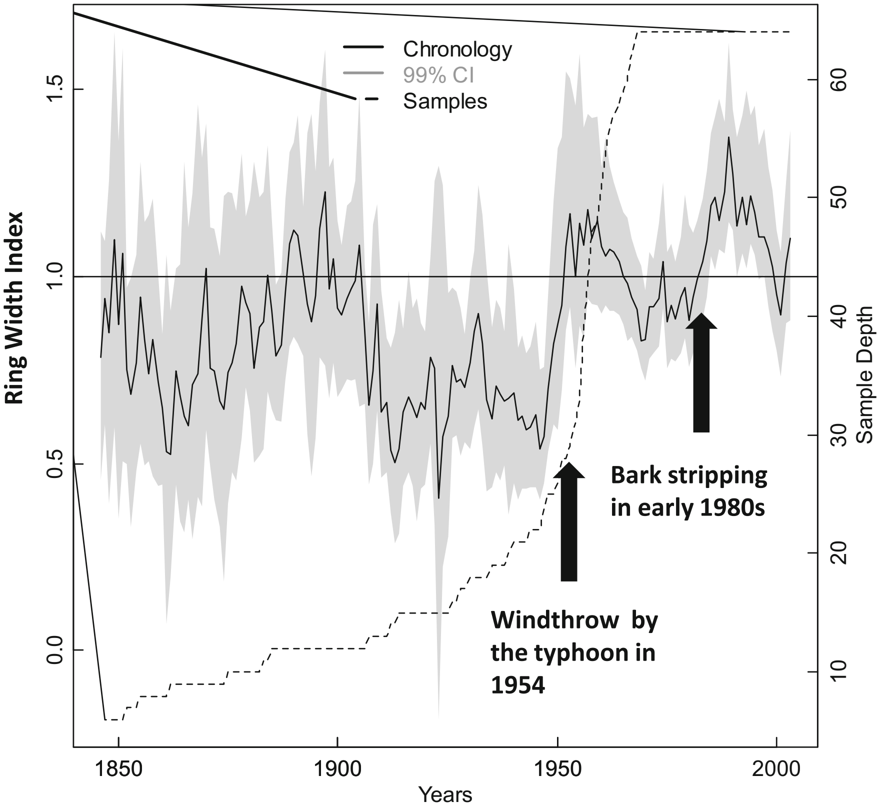

Fig. 16.13 Changes in annual ring growth by disk analysis of windthrows in 2004. Ring width index (RWI) showed the ratio of the average annual ring width for each year to the total average annual ring. Sample depth means number of sample trees

high deer population density, there is a risk that the expansion of land devoid of trees will progress at once due to the added effect of windfall caused by typhoons.

The DBH frequency distribution of sampled trees in 1984, when bark stripping was the most prominent, showed that most individuals had a DBH of 15–20 cm (Fig. 16.14). The distribution curve was mountain-shaped with few small-diameter trees—with the diameter of the smallest individual being 6.2 cm DBH. The relationship between the disk diameter and age in 1984 revealed that the period required for the diameter to reach a DBH of 6.2 cm was 27 years. Many of the smaller trees might have disappeared because of browsing and bark stripping by deer (Iijima and Nagaike 2015). Therefore, if deer are removed for about 30 years in a place that can become renewed forest, many of the renewed trees will grow to a DBH of 6 cm or more. Furthermore, even if deer invade afterward, most of these trees will remain and the forest will likely be maintained.

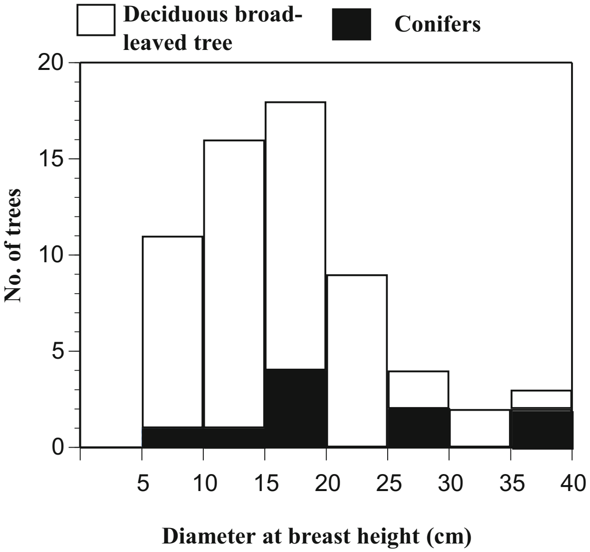

Fig. 16.14 Frequency distribution of diameter at breast height of sampled trees ($n = 65$) in 1984 (Miyaki 2011)

16.8 Deer Density and the Aim of Forest Management

Because the appropriate population density of deer varies greatly depending on forest management goals, the conservation of forest ecosystems can also be achieved simultaneously by combining various purposes.

16.8.1 Conservation of Rare Plants

The effect of deer browsing on vegetation was more significant for herbaceous and shrub species than for tall tree species (Table 16.2). In deer habitats with dense populations, the increase in deer first affects herbaceous plants, resulting in many plants becoming extinct before an increase in deer number was even noticed. Therefore, the deer need to be controlled and kept at a low density ($<20\%K$ in Table 16.2), especially when conserving rare herbaceous plants and intensively foraged spring plants in national parks.

16.8.2 Regeneration of Forest

It is necessary to maintain a sapling bank to regenerate the forest, but even relatively low-density deer populations can significantly affect sapling density (Gill 1992).

However, as seen in the forests of Nakanoshima Island, stands that require urgent regeneration of saplings are limited. In growing forests, the renewal of saplings is not necessary, regardless of the presence of deer.

Nevertheless, forests with low sapling density and many gaps in the forest may accelerate the collapse of forests, especially with the added damage from windfall caused by typhoons; thus, it is necessary to regenerate them urgently. When the edible plants disappeared, sika deer began to eat plants that they had not eaten before, such as plum yew. They became heavily dependent on litterfall throughout the year (Takahashi and Kaji 2001; Miyaki and Kaji 2004; Ueno et al. 2007; Chap. 17). As the deer became dependent on low-quality foods, body mass decreased and maturation was delayed (Kaji et al. 2009). Nevertheless, the high-density ($>$20 km2) deer population was sustained even under severe food limitations for a long time. Forest ecosystems are greatly affected when deer density is maintained close to the carrying capacity.

To restore the ecosystem, it is necessary to undertake intensive population control to reduce deer density and promote habitat management. This can be done through methods such as installing fences in the forest gaps to regenerate trees. It is essential to eliminate deer or reduce the density for approximately 30 years to maintain forest ecosystems. However, it should be noted that the effect of previous high deer density prolongs for decades (Nuttle et al. 2014) and the efficacy of the fence depends on the timing of fence establishment (Otsu et al. 2019, Chap. 26).

Furthermore, the interaction between understory vegetation and tree recruitment in relation to deer density should also be considered. Dense understory vegetation inhibits tree recruitment by shading and hides tree saplings from deer browsing (Uno et al. 2019). The relationship between deer density, understory vegetation, and tree saplings is complex because deer eat understory vegetation that may positively or negatively affect tree recruitment. Then, the amount of understory vegetation in addition to deer density should be considered for successful tree recruitment (Itô et al. 2014).

16.8.3 Sustainable Hunting

If the primary goal of hunting is maximum sustainable yield (MSY), the point at which the recruitment rate of the sika deer population is maximized and the deer density reaches close to half of the ecological carrying capacity ($K/2$) will be required. However, such a high density ($\geq 40\% K$) dramatically impacts the flora and forest structure (Kaji et al. 2010, Table 16.2). It is an effective method to use land with high densities of deer populations for hunting when the forest management goal is to maintain forest structure in a short duration of approximately 30 years. Considering the high risk of forest disturbance caused by typhoons, on forests that have already been deteriorated by long-term browsing by deer, it is recommended that sustainable hunting at a suitable deer population density be done to allow regeneration of the forest.

In addition, the appropriate management of deer populations and the period for their exclusion may differ depending on various goals, such as biodiversity conservation and forest soil conservation (Chaps. 23 and 27). As a result, it is necessary to clarify conservation and management goals and to consider appropriate approaches to meet these objectives.

Lessons from deer-vegetation interactions on Nakanoshima Island revealed that the sika deer population lacks a self-regulating mechanism, which would have been used to avoid an irreversible impact on vegetation (Kaji et al. 2010; Ueno et al. 2018). Therefore, for effective management in forests and ecosystems, the promotion of sustainable hunting, hunting as resource management tool, and culling for ecosystem management should be synergistically combined under adaptive management (Kaji et al. 2010; Chap. 32).

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Chapter 17
Irruptive Dynamics of Sika Deer: Search for the Mechanism

Koichi Kaji and Kazutaka M. Takeshita

Abstract To understand the process and mechanism of irruptive behavior, we reviewed previous studies on this behavior in two contrasting sika deer populations: an introduced population on Nakanoshima Island (NKI herd) and a naturally colonizing population on Cape Shiretoko (CS herd) and the consequences on the habitat over 30 years. Both populations had achieved peak abundance, followed by a crash (i.e., mass mortality) with the elimination of “surplus” forages, resulting in significant effects on the vegetation. However, there were marked differences in post-crash behavior between the two populations. Following the initial population reduction, the NKI herd recovered with a slower growth rate reaching a higher peak abundance than the first irruption, while the CS herd showed repeated irruptions and crashes with no decline in peak abundance. The NKI herd shifted their winter staple food from dwarf bamboo to woody vegetation and litterfall after that time. The nutrition of these alternative resources decreased in winter; however, they maintained a high nutrition level in summer as buffering resources, restricting starvation or malnutrition, and maintaining high reproductivity and survival of adult female deer. In contrast to the NKI herd, the CS herd had high-quality foods available throughout the year after the initial population crash, particularly a large amount of Gramineae herbs in summer and a limited amount of dwarf bamboo in winter, which was preserved under the snow. The carrying capacity differences between summer and winter and its combination with winter severity might generate oscillations while maintaining a high-quality population on CS. “Surplus” forages shape the initial irruption, and shifting to alternative resources, combined with snow accumulation generates various post-crash behaviors.

K. Kaji (✉)
Tokyo University of Agriculture and Technology (Retied), Fuchu, Japan
e-mail: kkaji@cc.tuat.ac.jp

K. M. Takeshita
Center for Health and Environmental Risk Research, National Institute for Environmental Studies, Tsukuba, Japan
e-mail: kazutaka.takeshita.0716@gmail.com

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17.1 Introduction

In large herbivores, the irruptive population models predict that when ungulate population densities are low in favorable habitats, they tend to increase rapidly to a peak, followed by a crash and then a recovery to a reduced carrying capacity (K) through a dampened oscillation (Caughley 1970) or a stable equilibrium (Leopold 1943; Riney 1964). Population irruptions of these species are mainly triggered by the following three critical driving factors: population confinement, habitat modification, and decrease in predation or hunting by humans, but this behavior is a complex and poorly documented phenomenon (McCullough 1997). Irruption of large herbivores is widely observed (Forsyth and Caley 2006); however, the post-population crash behavior have been reported in relatively few cases with closed habitats and exposure to harsh weather (Gross et al. 2010). Owen-Smith (2002a, b) used a metaphysiological modeling approach to evaluate the effects of heterogeneity in vegetation resources on the population stability of large herbivores. Those studies predicted that periods with low-quality forage stabilize herbivore population dynamics by providing a "reserve" when high-quality forage patches were depleted by buffering against extreme food depletion. Forsyth and Caley (2006) developed mathematical models that accommodate large herbivore irruptive dynamics by incorporating parameters relating to lag time and depletion of nonrenewable surplus resources into conventional irruptive dynamics models. "Surplus" forage is defined as accumulated biomass above and beyond annual vegetation growth, which is correlated to the likelihood and magnitude of an irruption (Gross et al. 2010). These parameters allowed us to describe large-herbivore irruptive dynamics in more detail. However, there are still some critical factors required for explaining irruptive dynamics, especially post-population crash dynamics, such as nutritional quality, quantity, and spatial distribution of food resources (Gross et al. 2010).

A previous report (Kaji et al. 2009) first reviewed case studies of the irruptive behavior of two contrasting sika deer populations: an introduced population on Nakanoshima Island (NKI herd) and a naturally colonizing population on Cape Shiretoko (CS herd) and the consequences on the habitat. Both populations attained peak abundance and then crashed, causing significant effects on the vegetation; however, there were marked differences in post-crash behavior between the two populations. Following the initial population crash, the NKI herd recovered with a slower growth rate and reached a higher peak population size than the first irruption, while the CS herd showed repeated irruptions and crashes with no decline in peak abundance (Kaji et al. 2009).

That study suggested that density-dependent resource limitation through interaction with winter climate was the critical limiting factor of peak abundance for both populations. The carrying capacity differences between summer and winter might generate different post-crash behaviors for the two contrasting populations, such as low-quality (NKI herd) and high-quality (CS herd) in terms of body size and reproduction (Kaji et al. 2009). However, the mechanisms that determine irruptive dynamics and sustain the high density of sika deer under food limitation are still unclear as food quality, quantity, and spatial distribution evaluations are lacking.

Based on long-term monitoring of the two populations over 30 years, we evaluated factors promoting irruptive dynamics of the NKI herd compared to the CS herd, focusing on "surplus" forage and vegetation changes. We updated the initial analyses of Kaji et al. (2009, 2010) based on recent information related to changes in food abundance and quality (Yoshizawa et al. unpublished data) and their effect on the population dynamics of NKI (Takeshita et al. 2015, 2016, 2018; Ueno et al. 2007, 2018) and CS (Kohira et al. 2011; Ishinazaka 2017).

17.2 Nakanoshima Island

17.2.1 Study Site

Nakanoshima Island, along with two islets, has a total area of 520 ha and is located in Lake Toya, southwestern Hokkaido, the northernmost island of Japan. The primary vegetation of Nakanoshima Island alone (497.8 ha) is composed of deciduous broad-leaved forest (457 0.1 ha, 91.8%), where the dominant species are *Acer mono* (painted maple) and *Tilia japonic*a (linden), a coniferous plantation (31.5 ha, 6.3%) of *Abies sachalinensis* (Sakhalin fir) and *Larix leptolepis* (Japanese larch), and open grassland (7.8 ha, 1.6%). This island is part of the wildlife reserve of Shikotsu-Toya National Park, and no predator for sika deer is present. Nakanoshima Island is characterized by mild winters. The most severe effect of selective foraging by deer occurred in the initial irruption phase when the highly palatable species of herbaceous plants, tree species, and dwarf bamboos (*Sasa senanensis* and *S. kurilensis*) were eliminated (Chap. 16). We confirmed two of 40 deer marked with ear tags migrated from the island to the surrounding mainland during 1980–1984 where one died from a traffic accident, and the other one was killed by a nuisance control procedure on the mainland. However, none of the 364 tagged deer was displaced from the island during 1992–2012 (Kaji et al. 2005; Ueno et al. 2018); thus, emigration and immigration were negligible.

17.2.2 Population Change

17.2.2.1 Drive Count

We monitored population changes in the deer on the island using drive counts of approximately 30 drivers and 2 observers on the boat in early March each year beginning in 1980 (Kaji et al. 1988). This method provides reliable information on population size at higher deer densities (5–22 deer/km^2) if a lower level of accuracy (within 20% or more) is acceptable (Borkowski et al. 2011). We evaluated the precision and accuracy of the drive count at a higher density (11–53 individuals/km^2, estimated by the mark-resight (MR) method) on the island compared to the MR method (Takeshita et al. 2016). The drive count numbers tended to be overestimated compared to those from the MR method; however, the trends were consistent, and there was a statistically significant positive relationship between the population estimates of the two methods (Takeshita et al. 2016), suggesting that drive count estimates are a useful population index, at least in these circumstances.

17.2.3 Population Irruption and Its Dynamic Phase

The population originally grew from three deer (one male and two females) introduced during 1957–1966 to a peak of 273 animals (52.5 deer/km^2) in March 1984, followed by a population crash ($n = 67$ deer) and removal ($n = 95$ deer), resulting in an estimated population size of 137 animals (26.3 deer/km^2) by May 1984 (Kaji et al. 1988). We derived a conservative pre-crash population estimate of 299 deer after the addition of 26 carcasses found prior to the drive count in March 1984 (Kaji et al. 1988). After the initial crash, the population recovered to a second peak of 434 animals (85.3 deer/km^2), 1.6 times higher than the first peak, in March 2001 (Kaji et al. 2009; Fig. 17.1).

We estimated the rate of population increase as an approximation of the intrinsic rate of increase (r_m) by least-squares linear regression after logarithmic transformation of population estimates (Caughley 1977). Although the first irruption of the NKI

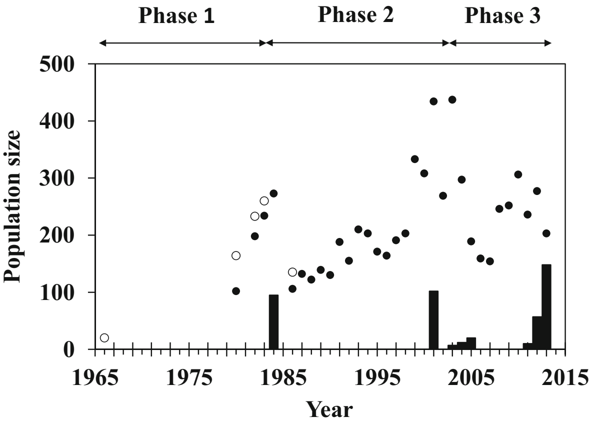


Fig. 17.1 Population changes of sika deer on Nakanoshima Island, Hokkaido, Japan, 1967–2013. The black bar shows the number of deer removed from the island in 1984 (95), 2002 (102), 2003 (7), 2004 (12), 2005 (20), 2011 (10), 2012 (57), and 2013 (148). The open circle shows the estimated population size, and the black circle shows the ground count. Phase 1, before May 1984; Phase 2, June 1984–May 2004; and Phase 3, after June 2004 to May 2013. Modified from Kaji et al. (2009), by adding data for the last few years

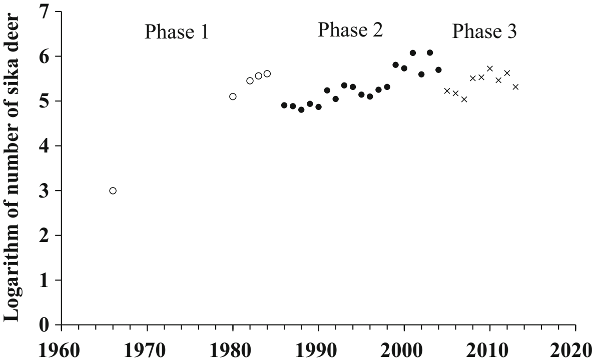


Fig. 17.2 Log-linear regression from 1966 through 1984 (Phase 1) indicating a 16% annual rate of increase ($r = 0.15$, $\lambda = 1.16$, $R^2 = 0.9979$), and from 1986 through 2001 (Phase 2) indicated a 7% increase ($r = 0.067$, $\lambda = 1.07$, $R^2 = 0.7498$). Xs show population size from 2005 to 2013 (Phase 3). Modified from Kaji et al. (2009) by adding data for the last few years

herd imposed an irreversible change on the vegetation, the population continued to increase with a lower growth rate (1986–2001: $r_m = 0.07$) than the first irruption (1964–1984: $r_m = 0.15$) (Kaji et al. 2009; Fig. 17.2). The population declined a second time to 304 animals (58.5 deer/km^2) by May 2001 due to natural mass mortality ($n = 42$ deer) and removal ($n = 102$ deer) but quickly recovered to 437 animals in March 2003, followed by a second crash with approximately 24% of the population naturally dying ($n = 114$ deer) in the winter of 2003–2004 (Kaji et al. 2009). By 2007, 154 animals (29.6 deer/km^2) remained and stabilized at a high density, averaging 48.7 ± 6.8 (SD) deer/km^2 from 2008 to 2013 (Fig. 17.2). The irruptive dynamics with decreasing population growth rate and increasing peak abundance in the second irruption compared to the initial irruption (Fig. 17.1) was consistent with the demographic analysis using a population structure estimated from age-at-death data in natural conditions (Takeshita et al. 2018; Fig. 17.3).

Based on the crash data, we divided the sika deer population dynamics into three phases, prior to May 1984 (Phase 1), June 1984–May 2004 (Phase 2), and June 2004–May 2013 (Phase 3: Figs. 17.1 and 17.2), which corresponded to shifting winter staple foods of the deer population (see below).

17.2.4 Changes in Food Habits

The food habits of the NKI herd were analyzed using rumen samples from deer dying from natural or accidental causes during 1980–1982 ($n = 11$; Phase 1) and 1993–1999 ($n = 55$; Phase 2) (Takahashi and Kaji 2001) as well as deer sacrificed for academic purposes from 2004 to 2005 ($n = 19$; Phase 3) (Ueno et al. 2007) (Fig. 17.4). During the initial population growth (Phase 1), winter rumen samples ($n = 9$) consisted of twigs and bark (48.5%), the broad leaves of deciduous trees

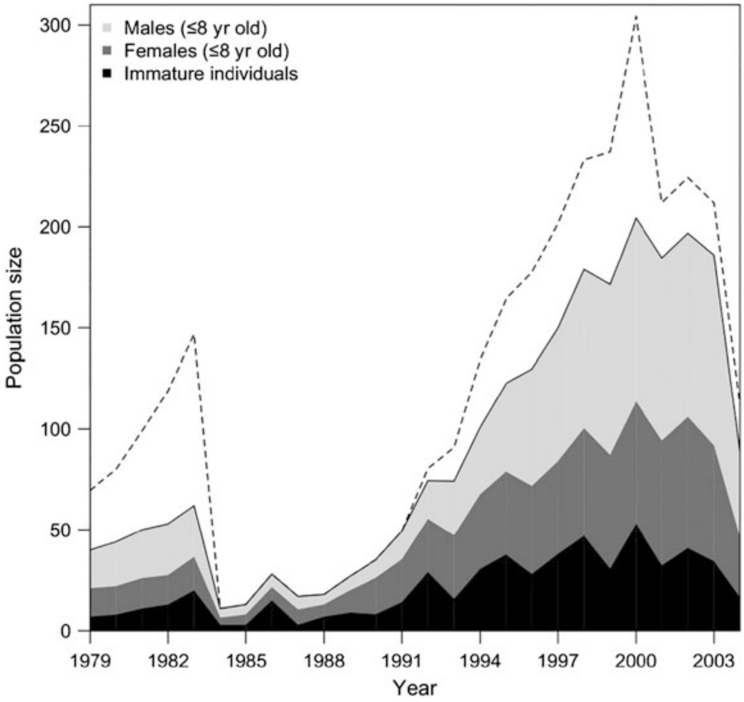


Fig. 17.3 Conditional age structure of a sika deer (*Cervus nippon*) population on Nakanoshima Island, Japan, every June 1 during 1979–2004 excluding human-caused deaths. The conditional age structure was estimated from individuals that died by 8 years of age. The population was classified into three groups (termed stages): immature (black), adult female (dark gray), and adult male (light gray). The total population size estimated from the conditional age structure, including human-caused deaths, is shown with a dashed line (Takeshita et al. 2018). This figure was originally published in Takeshita et al. (2018) and used under CC BY 3.0

(25.4%), and dwarf bamboos (11.7%). Spring samples ($n = 2$) contained a relatively higher ratio of graminoids (27.0%) and ferns (11.9%) (Fig. 17.4). After the initial irruption (Phase 2), the proportion of deciduous broad leaves in rumen was considerably high, even in spring (56%, $n = 13$) and summer (83.5%, $n = 8$), the seasons of fresh greens, suggesting that the deer depended on the litterfall in all seasons as the staple food. In addition to the litterfall, the percentage of the formally unpalatable but abundant cover plant *Cephalotaxus harringtonia* (plum yew) increased during winter (30.0%, $n = 10$) and spring (39.7%, $n = 13$). During Phase 3, litterfall occupied over 70% of rumen contents, except in winter 2004 when bark peeling from fallen trees after a typhoon was an available option (Ueno et al. 2007). Under heavy grazing and browsing, the deer shifted their winter staple foods from dwarf bamboos (initial irruption) to plum yew (*Cephalotaxus harringtonia*) and litterfall (second irruption) and finally to mainly litterfall (post second irruption). These results suggest that litterfall was the essential food resource all year round in Phases 2 and 3 (Takahashi and Kaji 2001; Miyaki and Kaji 2004; Ueno et al. 2007) and that

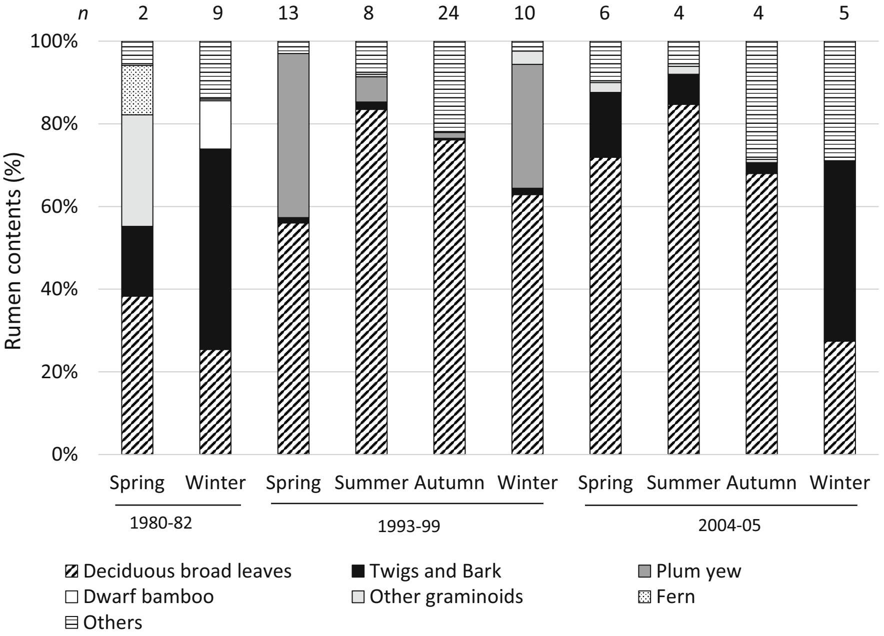


Fig. 17.4 Changes in the composition of rumen contents of sika deer on Nakanoshima Island, Lake Toya, in 1980–1982 (Phase 1), 1993–99 (Phase 2), and in 2004–05 (Phase 3). Modified from Takahashi and Kaji (2001) and Ueno et al. (2007)

the plasticity of food habits of sika deer shifts their staple foods to exploitation of alternative foods when their palatable food resources were eliminated by selective foraging (Takahashi and Kaji 2001).

17.2.5 Availability and Quality of the Staple Foods

We applied Aldous Browse Survey Method (Aldous 1944) to assess availability of understory vegetation (up to 2 m in height) between 1981 and 1983 (Kaji and Yajima 1992). We set up circular plots (4 m radius in 1981, $n = 60$; 3 m radius in 1982 and 1983, $n = 34$) at intervals of 30 m along randomly selected lines on the main island (Nakanoshima Island). The most dominant understory on the main island was dwarf bamboo (*S. senanensis*) in the early 1980s and plum yew by the mid-1990s. Dwarf bamboo occurred in 85% of the plots ($n = 60$) with an average cover of 56% in 1981 (Chap. 14); however, it was eliminated by the high-density deer population by 1983, which crashed in the following winter (Kaji et al. 1988). Plum yew, an unpalatable woody vegetation, occurred in the majority of plots (97–100%) with an average cover of 44–54% in 1982–1983 (Miyaki and Kaji, Chap. 14) and remained the dominant understory covering the majority (91.8%) of the island surface in 1994

(Miyaki and Kaji 2004). However, the coverage declined yearly, with an average cover of 11.7% in September 2004 (Takeshita et al. 2018). Although the winter of 2003–2004 was relatively mild, the most severe population crash (second population crush) occurred, coinciding with a significant reduction in plum yew (Kaji et al. 2009).

The total biomass and consumption of deer food by habitat type on the island were surveyed in July 1994 (Miyaki and Kaji 2004). Litterfalls accounted for 92.4% of the potential food supply and contributed 75.6% of the deer total consumption. Other plants were minor components of the feed.

Crude protein (CP) content of deer food plants on the island was analyzed as an indicator of diet quality to assess whether the alternative resources contributed to a decline in the quality of sika deer food (Yoshizawa et al. unpublished data). We collected dwarf bamboo (*S. senanensis*) and plum yew in exclosure fenced plots because deer had eliminated them. The CP content of dwarf bamboo was stable throughout the seasons (14.1–14.8%) and satisfied the body growth requirement (>13%; Robbins 1993) in all seasons. The CP content of plum yew and litterfall showed the same levels as dwarf bamboo in summer; however, they declined to 5–9% in autumn and winter, indicating a reduction in diet quality (Yoshizawa et al. unpublished data), but meeting the maintenance range (5–9%) (Robbins 1993).

17.2.6 Body Mass and Population Parameters

17.2.6.1 Body Mass

On Nakanoshima Island, we captured deer in spring (March–May) 1982–2005 and measured body mass using a bench scale, spring scale, and electronic scales. The mean body mass of females changed considerably during the study periods, with the most noticeable occurring in the initial irruption (Phase 1). Although the initial body mass and skeletal size approximated those of mainland deer between the pre-crash (1982) and post-crash (1984) periods, female body mass decreased by 29% for calves, 17% for yearlings, 9% for 2.5-year-olds, and 15% for ≥3.5-year-olds (Kaji et al. 1988). The lowest body mass was recorded in 2004 when the second population crash occurred, and between 1982 and 2004, the body mass of females decreased by 38% for calves, 37% for yearlings, 15% for 2.5-year-olds, and 26% for ≥3.5-year-olds (Kaji et al. 2009). The most significant reduction in body mass occurred in younger age groups (calves and yearlings), but corresponding changes occurred at all ages, suggesting that the negative effect of reduced food quality affected the entire population. Preliminary analyses suggested that significant changes in population density through repeated irruption and artificial removal from the island might be the main factors influencing the body mass of female deer in the following spring (Kaji and Uno 2006).

17.2.6.2 Reproduction

Sika deer generally first conceive when they are yearlings (Suzuki and Ohtaishi 1993). The fecundity rate of sika deer females in the eastern region of Hokkaido reached a high of 90%, with a slight annual variation for both yearlings and older females (Kaji and Uno 2006). On Nakanoshima Island in 1982, both a yearling and a 2.5-year-old female, killed during a capture attempt, were pregnant. During 1982 and 1984, the observation of female marked deer of known age ($n = 11$) showed that none of the 2.5-year-olds had calves (Kaji et al. 1988), suggesting that associated with body mass decline, the age at maturity was delayed from yearling to 2 years of age during 1982 and 1984 (Phase 1) (Kaji et al. 1988).

We surveyed the pregnancy rate of sika deer using ultrasonography for live female deer captured between 1988 and 2005 (Kaji and Uno 2006). We found that the age of maturity was further delayed to 3 years, and the pregnancy rate for adult females ($\geq$ 3 years old) varied between 50 and 90%, with a minimum of 50% observed during the second population crash (Kaji and Uno 2006). The tiny female deer with suppressed skeletal growth died due to dystocia even when they reached sexual maturity at 3 years of age (Takahashi et al. 2005).

17.2.6.3 Tooth Wear

Overgrazing, with its consequential food resource limitation, leads to a lower-quality diet that accelerates molar wear and reduces body mass and fat deposition by altering the consumption to larger quantities of rougher material (Tyler 1986; Skogland 1988; Kojola et al. 1998). High grazing pressure also causes dwarfing in herbs and increases the ingestion of soil particles, resulting in increased tooth wear (Skogland 1988; Takahashi et al. 1999; Takahashi and Kaji 2001; Loe et al. 2003).

The molar wear rates of the NKI herd were not different between sexes but were significantly higher in the post-decline phase (1985 or later) than the increasing phase (1982 or earlier), which was equivalent to the results in the control mainland population, suggesting that wear rates of the first molar increased with the decline in food quality (Takahashi et al. 1999). These findings were validated based on long-term monitoring, further demonstrating that the molar wear rates were the lowest in Phase 1 (before May 1984) and increased in Phases 2 (June 1984–May 2004) and 3 (after June 2004 to May 2013); the latter two phases were equivalent and the most accelerated among extant sika deer populations in Japan (Takeshita et al. 2015). In Phases 2 and 3, when deer were eating short greens and litterfall (fallen leaves), they ingested a considerable amount of soil, which appeared to be the main factor promoting the faster wear of molars in sika deer on Nakanoshima Island (Takahashi et al. 1999; Takeshita et al. 2015).

17.2.6.4 Survival Pattern

Survival monitoring data from radio-collars with mortality sensors were collected from 219 individuals (93 males and 126 females) from 2002 to 2012, and the sika deer survival rate and its influential factors were estimated (Ueno et al. 2018). The annual survival rates across sexes and age classes (calf, yearling, prime: aged 2–9 years old, and old: $\geq$ 10 years old) decreased with increasing population density, snow depth, and winter precipitation. The winter severity had a more significant effect on adult survival than density regulation. It was also found that adult female survival was maintained at a high level with a mean of 0.84 (95% CI: 0.80–0.88) (Ueno et al. 2018).

17.2.6.5 Factors and Life Stages Determining Irruptive Dynamics in Phase 1 and Phase 2

We evaluated the factors (deer density and snow accumulation) and stages in sex and age classes (immature, adult female, and adult male) that determine irruptive dynamics (Phase 1 and Phase 2) through key-factor/key-stage analysis of the population structure using age-at-death data of deer that died naturally ($n = 879$) during 1979–2013 (Takeshita et al. 2018). The most influential factor in deer population change was density in Phase 1; however, the contribution of this factor was reduced in Phase 2. Snow accumulation was not a prominent feature in Phase 1 (11.74%), and it decreased further in Phase 2 (0.64%). The largest contribution of sex and age classes also differed between Phase 1 (adult male) and Phase 2 (immature stage) (Takeshita et al. 2018). The adult female contribution to population change was the lowest in both phases, suggesting high stability in female survival (Takeshita et al. 2018), which was confirmed by the study on sika deer survival rate using radio-collars (Ueno et al. 2018).

17.3 Cape Shiretoko

17.3.1 Study Site

Sika deer recolonized the Shiretoko Peninsula in the early 1970s and have expanded their range and size since the mid-1980s, resulting in strong chronic effects on the natural vegetation of forests and grasslands on wintering grounds (Kaji et al. 2009). Long-term air count monitoring has been conducted for the wintering CS herd since 1986. We surveyed 5 km^2 of the sika deer winter range on CS, which was expanded to 7 km^2 as a management method for population control from 2007; however, it included the same feeding grounds. A recent study using radio-collared sika deer on CS showed that individuals of CS herd were residents (Ishinazaka 2017).

Cape Shiretoko is characterized by cold winters with heavy snowfall and ice floes, deciduous and coniferous mixed forests, and extensive grassland dominated by dwarf bamboo and Gramineae herbs such as reed grass (*Calamagrostis langsdorfii*), and it is inhabited by a potential predator, the brown bear (*Ursus arctos*). In recent years, grassland vegetation has been strongly influenced by chronic grazing by sika deer, causing changes in species composition and dwarfing of herbs.

The vegetation of the CS study site is characterized by a coastal plateau meadow (84 ha, 16.8%) and deciduous and coniferous mixed forests (416 ha, 83.2%). The plateau grassland consists of 49.7 ha (59%) of *Sasa* dominated by *S. senanensis* and 28.0 ha (33%) of plagiosere succession dominated by unpalatable plants and grasses with high foraging tolerance (Hokkaido Regional Forest Office 2009). Since the Shiretoko Peninsula (Shiretoko National Park and peripheral areas) was designated as a UNESCO World Natural Heritage Site in 2005, managing the overabundant deer population is a significant concern (Chap. 32).

17.3.2 Population Change

The naturally colonizing deer population on CS in the early 1970s showed repeated irruptive behavior with no apparent decrease in peak abundance, which reached the first peak of 592 animals in 1998, the second peak of 626 in 2003, and the third peak of 603 in 2005 (Fig. 17.5; Kaji et al. 2009). However, the winter peak abundance decreased to 524 animals in 2006 and 518 in 2007. Population control began from the winter of 2007–2008, when a total of 883 deer (469 adult females, 277 adult males, 129 calves, and 8 with unknown sex and age) were culled during 2007–2019 based on the "Conservation and Management Plan for Sika Deer in Shiretoko Peninsula" leaving 52 animals in 2019 (Shiretoko Nature Foundation 2020). Intensive female culling led to success in the population reduction of CS (Fig. 17.5).

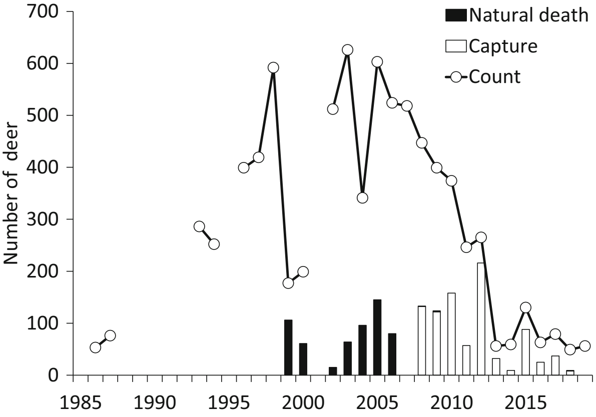


Fig. 17.5 Changes in the sika deer population on Cape Shiretoko, Hokkaido, during 1986–2019, based on aerial photographic censuses. Modified from Kaji et al. (2004), Ishinazaka (2017), and Ministry of the Environment (unpublished data). Population control started in FY2017. The 2008 and 2009 observations include the pre-wintering culling numbers of 33 and 50 deer, respectively

17.3.3 Vegetation Change

Associated with the increasing deer population, the composition and structure of forests and vegetation communities in grasslands changed dramatically due to heavy grazing and browsing. The tall plants such as *Angelica* spp. decreased to near extinction. In contrast, unpalatable plants (*Senecio cannabifolius* and *Ligularia hodgsonii* (Compositae)) and invasive plants (*Cirsium vulgare* (bull thistle)) greatly expanded their range (Tokida et al. 2004). The dwarf bamboos in the forest disappeared, the available browsing covers were eliminated, and bark stripping from palatable tree species such as elm (*Ulmus laciniata*) and large oak (*Quercus crispula*) increased (Kaji et al. 2009). The order of density-dependent vegetation changes in CS followed the same pattern as NKI (Chap. 16), with the most significant vegetation changes in the initial irruption on both CS and NKI.

17.3.4 Availability and Nutritional Quality of the Staple Food

The CS herd had available a large amount of Gramineae herbs (foraging-tolerant spp.) on the plagiosere succession community (28.0 ha, 33.3%) in summer and a limited amount of dwarf bamboo (*S. senanensis*) on the *Sasa* community (49.7 ha, 59.2%) in winter on a plateau grassland (84.0 ha) (Shiretoko Nature Foundation 2009). The availability of dwarf bamboo during winter was restricted by annual snow accumulation.

In order to estimate standing crop and consumption of Gramineae herbs, mobile cages were set up in August 2007, and a mowing survey (50 cm × 50 cm) was conducted in October of the same year. After the cages were moved in August 2008, a mowing survey was conducted again in October of the same year. In the control plot with similar vegetation outside the cage, the aboveground parts that grew in the current year were mowed, and the standing crop in the cage was used as the production during the set period, and the difference between the standing crops in the cages and the control plots was used as intake ratio during the set period, and the dry weight was measured (Shiretoko Nature Foundation 2009). The standing crop of grasses (grasses in the cage) was 361.1 ± 14.9 g/m^2 (average ± SE, $n = 4$) in 2007 and 441.7 ± 31.1 g/m^2 ($n = 5$) in 2008, and the average intake ratio of the two summer months were 35% and 26.3%, respectively. The relatively small intake ratios suggested that CS had a margin in the summer carrying capacity.

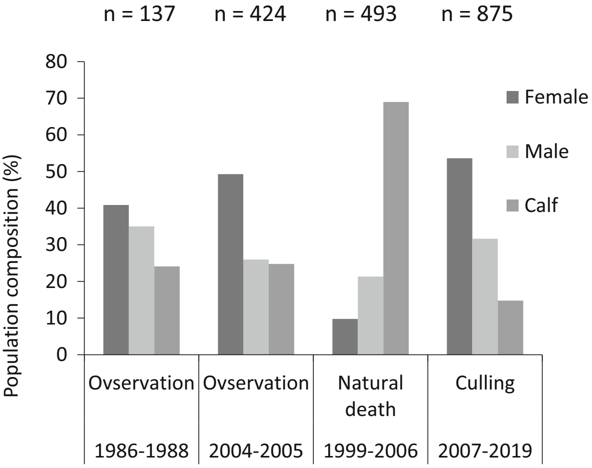
In order to investigate the effects of deer browsing on *S. senanensis*, three 100 m lines (6 survey plots of 2 m × 2 m at 20 m intervals per line) were established in the *S. senanensis* community on CS in 1999. In October 2007 and August 2008, the coverage and the culm height in each 1 m × 1 m plot was measured. In each 1 m × 1 m subplot of 2 m × 2 m plots in the line transect, we surveyed the cover and the height of the stems. The coverage of *S. senanensis* in October 2007 of 69.0 ± 1.1% increased 1.2 times in August 2008 to 84.9 ± 1.1% ($n = 72$), and the culm height increased 1.3 times from 38.3 ± 0.8 cm in October 2007 to 48.5 ± 1.0 cm in August 2008 ($n = 72$) (Shiretoko Nature Foundation 2009). These increases in Gramineae herbs and *S. senanensis* in 2008 suggested a reduction in grazing and browsing pressure by deer on the grassland through the first-year culling experiment.

Gramineae herbs and dwarf bamboo (*S. senanensis*) have been reported as high nutrient (CP) resources with nutritional values similar to those of pasture grass (Masuko and Souma 2009).

17.3.5 Body Mass and Population Parameters

We surveyed the population structure of deer on CS from ground observation each spring in late April 1986–1988 and photographic air counts in early February 2004–2005 and pooled data from multiple years and compared between the two periods (Kaji et al. 2004, 2009). A comparison between the population structure of the CS herd in 1986–1988 (86 males:100 females:59 calves, $n = 137$) and 2004–2005 (53 males:100 females:50 calves, $n = 424$) revealed that the sex ratio shifted greatly toward females; however, no significant changes in calf-to-female ratios were observed between the two periods (Kaji et al. 2009; Fig. 17.6). Over-winter mortality on CS herd during 1999–2006 (excluding 2000 with no data), consisted of 567 animals (48 adult females, 105 adult males, 340 calves, and 74 of unknown sex and age), composed mainly of calves (69%) and adult males (21%), with few adult females (10%) (Fig. 17.6; Kaji et al. 2009; Kohira et al. 2011) leading to a biased sex ratio toward females in the population structure. There was an extreme lack of animals aged 5 years or younger, especially in the cohorts born in 2004 and 2005, in CS and its neighboring Raus district, strongly suggesting that

Fig. 17.6 Sex and age composition from observation (1986–1988, 2004–2005) (Kaji et al. 2009), natural death (Kohira et al. 2011), and culling (2007–2019) (Shiretoko Nature Foundation 2020)



winter climate with combined habitat deterioration was the primary mortality source for calves (Kohira et al. 2011).

Adult male cast antlers collected between 1984 and 1987 and those of adult males dying from natural causes during 1999 were larger than those of harvested males in eastern Hokkaido, suggesting no decline in body size and mass during the initial irruption (Kaji et al. 2009). The pregnancy rates of yearlings and older females from spring culling in 2008 and 2009 were very high at 98% ($n = 61$) and 97% ($n = 38$), respectively (Shiretoko Nature Foundation 2008; Kushiro Nature Conservation Office, Ministry of the Environment 2011).

17.4 Discussion

17.4.1 Surplus Forage and Alternative Food

The initial phase in the irruptive population dynamics of NKI and CS herds was a simple dynamic in which the first crash coincided with the elimination of "surplus" forage such as dwarf bamboos and woody plant species in the forest (Kaji et al. 2009). On NKI, the sika deer showed plasticity in food habits by shifting the staple foods to alternative low-quality foods such as plum yew and litterfall under conditions of food limitation (Takahashi and Kaji 2001). In contrast to the NKI herd, the CS herd could not use fallen leaves due to heavy snowfall, but they can use high-quality foods: many graminoids in summer and a limited amount of dwarf bamboo in winter, which are preserved under snow. The carrying capacity differences between summer and winter combined with winter severity could generate oscillations while maintaining a high-quality population on CS. These results demonstrated that "surplus" forages shape the initial irruption (Forsyth and Caley 2006) and shifting to alternative resources generates post-crash behavior (Takeshita et al. 2018).

17.4.2 Vegetation Change

The effect of vegetation changes involves considerable variation in forage quality, accessibility, and regeneration (Gross et al. 2010). An increase in less-nutritious components could buffer resources that reduce mortality (Hobbs and Gordon 2010).

The process of vegetation changes and its consequences in the initial irruption and population crash in NKI and CS were considerably similar (Kaji et al. 2009); however, the irruptive behavior in the post-initial crash was extremely different. On NKI, plum yew as an alternative woody resource might allow deer to reach a higher peak in the second irruption than in the initial irruption due to increased availability, as the height and flexible stem provide browsing access, even under heavy snowfall (Takeshita et al. 2018). The combined effects of snow depth and vegetation height are particularly significant in determining the winter diet composition of sika deer populations (Seto et al. 2015).

There are contrasting landscapes on NKI and CS in terms of less or more snow, and small, heavily grazed grassland (1.6% of the study area) or extensive, highly productive grassland (16.8% of the study area). NKI herds could shift to alternative resources, such as woody vegetation and litterfalls, as buffering resources. The staple food changed from high-quality food (dwarf bamboo) with limited abundance in Phase 1 to abundant low-quality food such as plum yew and litterfall in Phase 2 and litterfall in Phase 3 (Yoshizawa et al. unpublished data). After the initial irruption, the molar wear rate in the NKI herd was the most accelerated (Takeshita et al. 2015), and body mass decreased; however, a high adult female survival rate was maintained (Ueno et al. 2018) with a relatively high pregnancy rate, causing a persistent high-density population. Summer litterfall may support increased nutritional demands associated with lactation and accumulation of body reserves because the high quality and abundant digestible energy of summer food are critical to winter survival (Parker et al. 1999). In addition, feeding on litterfall in winter was not restricted, with little snowfall on the island, contributing to a high deer density population.

High-density sika deer populations were also maintained in heavily browsed habitats using litterfall year-round on Yakushima Island, Kagoshima Prefecture (Agetsuma et al. 2011), and in the Tanzawa Mountains, Kanagawa Prefecture (Kaneko et al. 2020). Depending on litterfall all year sustains a high density which might inhibit forest regeneration, as well as decrease palatable species, increase unpalatable plants, and reduce forest floor vegetation diversity (Tremblay et al. 2005; Miyaki and Kaji 2009).

17.4.3 Density-Dependent Effect on Life History Parameters

In the NKI herd, there was a negative relationship between spring body mass in each age class and the previous winter population count, suggesting density-dependent changes in body mass under resource limitation (Kaji et al. 2009). However, shifting to alternative resources such as woody vegetation (plum yew) combined with litterfall reduced the density-dependent resource limitation and its effect on population growth. Consequently, such changes led to an increased carrying capacity after the initial population crash (Takeshita et al. 2018).

Vegetation also changed substantially on CS; the CS herd was a high-quality population characterized by a high adult female survival rate and pregnancy rate, stable calf:female ratio, as well as good antler growth. Density-dependent effects on body size (hindfoot length) appeared only after approaching the carrying capacity on CS (Murakami et al. unpublished data). These findings suggest that the overall density-dependent effects of sika deer only occurred when approximating the carrying capacity (Kaji et al. 2010).

17.5 Conclusion

"Surplus" forages shape the initial irruption, and the shift to alternative resources combined with snow accumulation generates various post-crash behavior. Natural regulation cannot be expected for sika deer, which have a weak density dependence on population growth and the plasticity of food habits, causing a significant impact on ecosystems (Kaji et al. 2010). Thus, after the initial population crash, alternative resources promoted different irruptive behaviors expected than the classic paradigm proposed by Caughley (1970) and Riney (1964).

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Chapter 18
Food Habits and Body Condition of the Sika Deer Population in the Tanzawa Mountains, Central Japan

Kazutaka M. Takeshita, Mizuki Kaneko, and Koichi Kaji

Abstract We reviewed studies on population density, food habits, and body condition of the sika deer population in the Tanzawa Mountains, central Japan, to understand the backgrounds of sustaining the high-density deer population in this heavily browsed habitat. Since the culling program under the Kanagawa Prefecture sika deer management plan commenced in 2003, the estimated total number of sika deer within the entire area of the Tanzawa Mountains has shown a decreasing trend. However, in some areas where the deer density estimates locally exceeded 20 individuals/km^2 in 2015, the understory vegetation was still deteriorating. An analysis of the diet composition of sika deer using rumen content samples collected during 2015–2016 revealed that the sika deer population largely depended on canopy subsidies such as fallen leaves in all seasons. These food items are known to be stably abundant even under intensive browsing pressure by sika deer. Moreover, the crude protein content values of the rumen content samples satisfied its minimum requirement estimates for maintenance even in the winter. Along with the progress of the culling program, winter body mass and hindfoot length of fawns in the Tanzawa Mountains increased. In the winter of 2014–2015, these body condition indicators reached a similar level to another Japanese sika deer population that lived in habitats relatively less deteriorated than the Tanzawa Mountains. We concluded that canopy subsidies were likely a contributing factor in sustaining the high-density sika deer population in a heavily browsed habitat.

K. M. Takeshita (✉)
Health and Environmental Risk Division, National Institute for Environmental Studies, Tsukuba, Japan
e-mail: kazutaka.takeshita.0716@gmail.com

M. Kaneko · K. Kaji
Tokyo University of Agriculture and Technology, Fuchu, Japan
e-mail: ikuzimo05@gmail.com; kkaji@cc.tuat.ac.jp

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18.1 Introduction

There have been some reports on high-density deer populations in heavily browsed habitats (e.g., a white-tailed deer (*Odocoileus virginianus*) population on Anticosti Island, Canada (Simard et al. 2008); a black-tailed deer (*Odocoileus hemionus sitkensis*) population on the Haida Gwaii archipelago, Canada (Le Saout et al. 2014); and sika deer (*Cervus nippon*) populations on Nakanoshima Island (Kaji et al. 2009) and Yakushima Island, Japan (Agetsuma et al. 2011)). The mitigation of density-dependent resource limitation using canopy subsidies as alternative food resources has been suggested as one of the key factors sustaining high-density deer populations in heavily browsed habitats.

"Canopy subsidies" were defined as the biomass from the canopy involving leaves, twigs, and acorns (Miyaki and Kaji 2004; Tremblay et al. 2005; Giroux et al. 2016; Takeshita et al. 2018). The annual availability of canopy subsidies is stably abundant and is roughly independent of the browsing pressure intensity of deer, which enable to maintaining high-density deer populations. For example, a white-tailed deer population on Anticosti Island has sustained their population density at high by using low-quality litterfall from balsam fir (*Abies balsamea*) (Tremblay et al. 2005; Lefort et al. 2007). In addition to the stable availability of litterfall, the use of litterfall may be related to the plasticity of the deer digestive system for enhancing the ability to digest low-quality forage (Bonin et al. 2016). The importance of canopy subsidies on sustaining the population density of white-tailed deer had already been noticed over 20 years ago (Ditchkoff and Servello 1998). Also in sika deer, a sika deer population on Nakanoshima Island has maintained their population density at about 50 individuals/km^2 by using fallen leaves throughout the year after a reduction in the availability of other food items such as dwarf bamboos and woody shrub (Chap. 17). However, few studies have examined the quantitative and qualitative contribution of canopy subsidies to the diet and body condition of sika deer (for a notable exception, see Kaji et al. (2009)).

In this chapter, we reviewed studies on population density, food habits, and body condition of the sika deer population in the Tanzawa Mountains, located in the northwestern Kanagawa Prefecture, central Japan, to contribute to an in-depth understanding of the backgrounds of sustaining high-density sika deer populations in heavily browsed habitats. In the Tanzawa Mountains, an increasing and expanding sika deer population has caused severe damage to forest ecosystems and human economic activities (Kanagawa Prefecture 2017). The understory vegetation was deteriorating due to the continuous browsing pressure by the sika deer population (Kanagawa Prefecture 2017).

18.2 Tanzawa Mountains

The Tanzawa Mountains (743 km^2) are located in the northwestern part of Kanagawa Prefecture, Japan (Fig. 18.1). The area rises from 8 to 1673 m above sea level (a.s.l.). The climate of the area is rainy and temperate. According to the Automated Meteorological Data Acquisition System located in the southwestern part of the Tanzawa Mountains (35°24′36″ N, 139°2′36″ E, 330 m a.s.l.; Japan Meteorological Agency 2019), yearly precipitation during 2004–2016 ranged from 1561 to 3241 mm (the minimum and maximum yearly precipitation values were recorded in 2005 and 2011, respectively). The 30-year average maximum snow depth during 1981–2010 was below 30 cm (Japan Meteorological Business Support Center 2012).

The majority of the Tanzawa Mountains (70.5%) consisted of forests; shrubs and bamboo occupied 1.4% of the total land; residential areas, agricultural lands, grasslands, and open water occupied 15.0%, 9.5%, 2.1%, and 1.5% of the total land, respectively (land cover data was obtained from the Natural Environment Information GIS, http://www.biodic.go.jp/trialSystem/EN/vg/vg.html, Accessed 10 Oct 2020). The urban landscape was mainly located in the southern and eastern parts of the Tanzawa Mountains. The dominant forest species varied depending on altitude (Kanagawa Prefecture 2017); conifer species plantations (*Chamaecyparis obtusa* and *Cryptomeria japonica*) mainly occupied the forests in low-altitude areas (≤800 m a.s.l.), while deciduous and evergreen broad-leaved species belonging to genera *Castanopsis*, *Quercus*, and *Fagus* mainly occupied the forests in high-altitude areas (>800 m a.s.l.). In the forest areas, intensive browsing pressure by

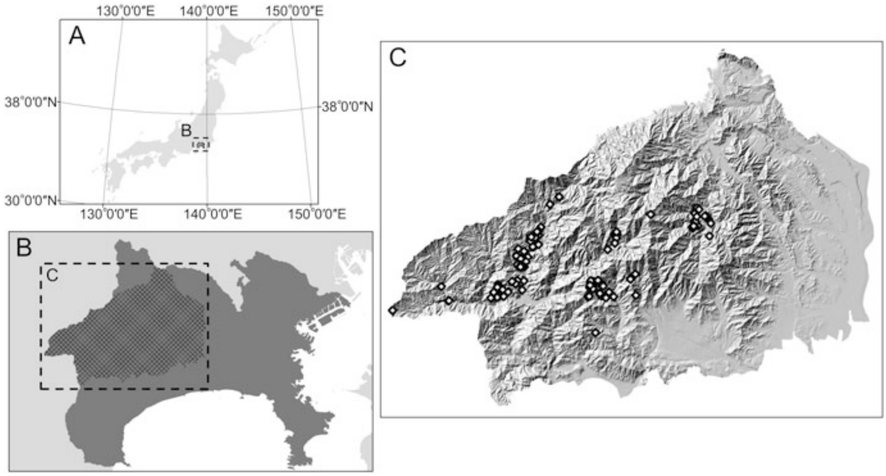

Fig. 18.1 (**a**) Map of Japan showing the location of the Kanagawa Prefecture (dark gray area). (**b**) Map of the Kanagawa Prefecture (dark gray area) showing the location of the Tanzawa Mountains (cross-hatched area). (**c**) Hillshade map of the Tanzawa Mountains. The rhombuses indicate the sampling points of sika deer rumen contents. The original data was from Kaneko et al. (2020)

Fig. 18.2 View of deciduous broad-leaved forest in spring at the Tanzawa Mountains (photographing date: 13 May 2015)

sika deer formed a browsing line (Forestry Agency of Japan 2012), indicating the limited availability of understory vegetation as food resources for sika deer in the Tanzawa Mountains (Fig. 18.2).

In the Tanzawa Mountains and the surrounding area, the Kanagawa prefectural government commenced the "Kanagawa Prefecture sika deer management plan" in April 2003 (April is the start of the fiscal year (FY) in Japan) (Kanagawa Prefecture 2003). The Kanagawa prefectural government has conducted a culling program under this management plan by mainly using the two following hunting methods: drive hunting, which involves chasing and barking by hunting dogs, and stalk hunting, which involves stalking by a sole hunter (Kanagawa Prefecture 2017; Chap. 33). These hunting operations are conducted regardless of the season, except for the extremely hot season (Yamaguchi et al. 2020).

18.3 Sika Deer Density

The estimated sika deer population size in the Tanzawa Mountains reduced from ca. 6200 to 4300 individuals between the end of FY2004 and FY2014 owing to the intensive culling program (Kanagawa Prefecture 2017). On the other hand, the program has resulted in both increases and decreases in deer density in different areas within the Tanzawa Mountains (Takeshita et al. 2017, 2019); there were some areas where the estimated deer density locally exceeded 20 individuals/km^2 at the end of FY2014 (the maximum was 53.7 individuals/km^2; Takeshita et al. 2017). Therefore, the understory vegetation has been deteriorating (Kanagawa Prefecture 2017, also see Chap. 26).

18.4 Diet Composition of Sika Deer

Twelve years after starting the management plan in 2003, Kaneko et al. (2020) collected rumen content samples from 126 culled sika deer to evaluate the diet composition of the sika deer population in the Tanzawa Mountains from May 2015 to June 2016. There was an apparent seasonal variation in the diet composition of the sika deer population (Fig. 18.3); however, the occupancy ratios of canopy subsidies (deciduous tree leaves, evergreen tree leaves, woody tissues (e.g., twigs, bark, and dead leaves), and acorns), especially, those of woody tissues, were constantly high irrespective of the season (Table 18.1). In Kaneko et al. (2020), the season was defined following Borkowski and Furubayashi (1998): spring (May to June), summer (July to September), autumn (October to December), and winter (January to April). In the winter, the season with the most severe food limitation in Japan, the sika deer population showed a notably high dependency on evergreen tree leaves compared with the other three seasons (Fig. 18.3, Table 18.1). Leaves of *Quercus salicina*, *Q. glauca*, *C. obtusa*, *C. japonica*, *Cephalotaxus harringtonia*, and *Tsuga sieboldii* were found in some of the winter rumen content samples. As crown heights of mature trees of these plant species were higher than sika deer browsing line in the Tanzawa Mountains (approx. Two meters in height), the sika deer population was likely to consume fallen leaves. Before starting the management plan, dwarf bamboo (*Sasa borealis* and *S. hayatae*) was a staple winter food for sika deer in the Tanzawa Mountains (Furubayashi and Maruyama 1977; Mitani et al. 2005). However, the occupancy ratio of dwarf bamboo was low in the winter of 2015–2016 (Table 18.1), because of the declining availability of the dwarf bamboo by the browsing pressure of sika deer (Yamane et al. 1997), which did not recover until 2016 (Kanagawa Prefecture 2017).

The diet compositions of sika deer in summer and autumn were not significantly different (Fig. 18.3), probably reflecting the summer sampling period (from September 12 to September 26, it corresponded to the late summer in the Tanzawa Mountains). When deer deposit reserves for overwintering in late summer and autumn, the sika deer population more depended on acorns and woody tissues than in other seasons (Fig. 18.3, Table 18.1). Acorns are known as one of "pulse resources," whose availability increases temporarily and abruptly. The contribution of pulse resources to overwinter survival and body condition in the following spring has been reported in some mammal species such as wild boar (*Sus scrofa*) (reviewed by Ostfeld and Keesing 2000). As for woody tissues, other Japanese sika deer

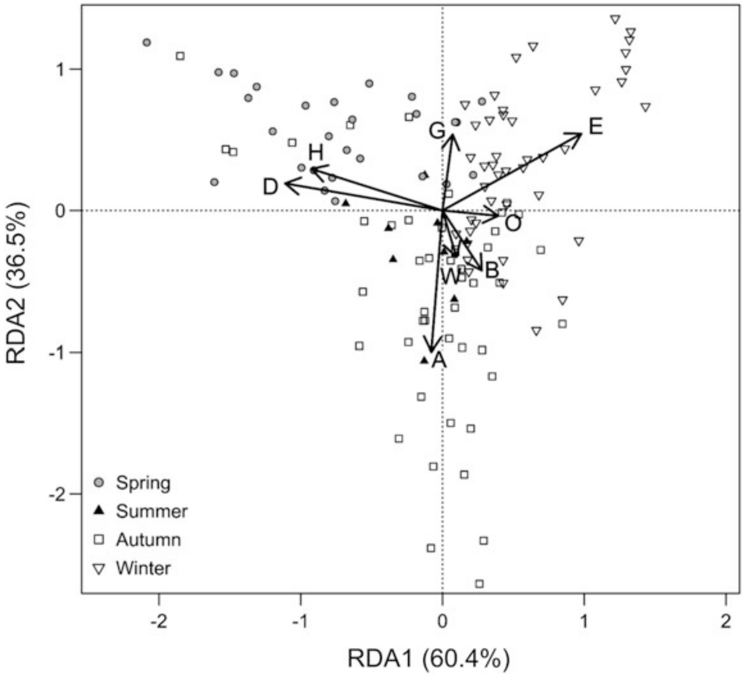

Fig. 18.3 Ordination of the diet composition of a sika deer population in the Tanzawa Mountains, using the results of the partial redundancy analysis performed in Kaneko et al. (2020). Gray circles, black triangles, open squares, and open down-pointing triangles indicate samples collected in the spring, summer, autumn, and winter, respectively. Arrows indicate factor loading of the occupation ratios of each food-item category (*H* herbaceous plants, *B* dwarf bamboo, *G* graminoids, *D* deciduous tree leaves, *E* evergreen tree leaves, *W* woody tissues, *A* acorns, *O* others). The variations in the diet composition derived from altitude (it was associated with vegetation differences in the Tanzawa Mountains) and sex-age class of deer were partialed out before the ordination. The original data was from Kaneko et al. (2020)

populations has been reported to often use twigs, bark, and dead leaves, which classified into the "woody tissues" category (Kaneko et al. 2020), as low-quality alternative resources during the winter season (Takahashi and Kaji 2001; Ueno et al. 2007; Agetsuma et al. 2011; Seto et al. 2015). It is a noteworthy finding that the sika deer population in the Tanzawa Mountains largely depended on these food resources even during the late summer and autumn seasons (Table 18.1). Such high dependency on woody tissues probably reflected the considerably deteriorated habitat condition of the study area.

In the spring, the season of fresh greens in Japan, the diet composition of sika deer was characterized by a higher dependence on herbaceous plants and deciduous tree leaves than in other seasons (Table 18.1, Fig. 18.3). Some of the canopy subsidies (deciduous tree leaves and woody tissues) accounted for a certain proportion of the sika deer diet (Table 18.1). The sampling period of sika deer rumen contents ranged over the springs of two different years (2015 and 2016); however, there was no

Table 18.1 Mean occupancy ratios (%) of eight food-item categories in the Tanzawa Mountains, Japan. Values in parentheses are standard deviation. Values are shown in each altitude level, season, and sex-age class because it was expected that the diet composition of sika deer would vary depending on altitudinal differences (these are associated with vegetation differences in the Tanzawa Mountains) and on sex and age differences. The original data was from Kaneko et al. (2020)

(a) Low altitude (≤800 m above sea level)

	Spring			Summer			Autumn			Winter		
	Fawn ($n^{a} = 1$)	Female ($n = 7$)	Male ($n = 9$)	Fawn ($n = 1$)	Female ($n = 4$)	Male ($n = 4$)	Fawn ($n = 4$)	Female ($n = 18$)	Male ($n = 15$)	Fawn ($n = 7$)	Female ($n = 18$)	Male ($n = 11$)
Herbaceous plants	3.92 (–)	15.33 (13.82)	22.55 (13.73)	0.44 (–)	10.48 (6.74)	6.33 (6.45)	9.67 (13.08)	4.08 (6.27)	1.65 (2.56)	1.08 (1.01)	1.03 (1.15)	0.32 (0.50)
Dwarf bamboo	0.00 (–)	0.00 (–)	0.02 (0.07)	6.89 (–)	6.39 (11.12)	6.93 (7.59)	12.95 (16.18)	9.36 (14.51)	15.43 (22.23)	6.30 (7.79)	7.83 (18.39)	11.01 (18.54)
Graminoids	2.21 (–)	22.40 (19.27)	15.12 (13.89)	5.56 (–)	16.03 (11.07)	29.32 (14.07)	2.87 (3.95)	6.64 (8.31)	13.86 (15.33)	28.22 (25.33)	16.59 (17.68)	11.72 (16.26)
Deciduous tree leaves	33.33 (–)	24.66 (11.10)	29.69 (16.03)	2.89 (–)	9.64 (8.27)	5.61 (10.32)	14.14 (23.25)	12.01 (18.24)	3.29 (4.84)	0.00 (–)	0.00 (–)	0.00 (–)
Evergreen tree leaves	0.25 (–)	0.07 (0.18)	0.20 (0.52)	0.00 (–)	0.00 (–)	0.41 (0.67)	0.12 (0.23)	1.94 (4.61)	0.05 (0.18)	12.63 (12.07)	19.33 (26.34)	39.64 (26.99)
Woody tissues (twigs, bark, and dead leaves)	59.8 (–)	35.07 (14.54)	27.87 (17.89)	68.89 (–)	35.79 (13.47)	25.63 (12.92)	35.00 (28.28)	50.07 (29.82)	40.43 (33.63)	36.87 (24.76)	47.45 (26.77)	30.11 (20.31)
Acorns	0.00 (–)	0.00 (–)	0.11 (0.24)	2.67 (–)	15.30 (14.22)	20.30 (2.77)	21.70 (24.80)	10.52 (14.70)	20.66 (22.40)	1.87 (3.04)	1.85 (3.69)	1.30 (1.30)
Others (e.g., conifer tree and fern leaves)	0.49 (–)	2.47 (1.15)	4.44 (6.52)	12.67 (–)	6.37 (3.81)	5.48 (4.13)	3.54 (1.35)	5.38 (7.01)	4.64 (5.79)	13.02 (8.41)	5.92 (4.50)	5.91 (4.74)

(b) High altitude (>800 m above sea level)

	Spring			Summer			Autumn			Winter		
	Fawn ($n = 0$)	Female ($n = 3$)	Male ($n = 7$)	Fawn ($n = 0$)	Female ($n = 0$)	Male ($n = 0$)	Fawn ($n = 1$)	Female ($n = 5$)	Male ($n = 4$)	Fawn ($n = 1$)	Female ($n = 3$)	Male ($n = 3$)
Herbaceous plants	–	29.96 (17.00)	5.62 (5.43)	–	–	–	0.68 (–)	19.97 (30.92)	0.93 (0.77)	7.97 (–)	0.39 (0.27)	3.59 (4.47)
Dwarf bamboo	–	0.00 (–)	0.07 (0.18)	–	–	–	0.00 (–)	0.00 (–)	9.47 (11.05)	3.23 (–)	0.00 (–)	0.16 (0.27)
Graminoids	–	27.95 (18.36)	56.94 (28.81)	–	–	–	3.2 (–)	26.90 (24.85)	9.52 (12.96)	16.38 (–)	89.98 (2.53)	32.37 (31.76)
Deciduous tree leaves	–	10.67 (5.22)	16.52 (29.03)	–	–	–	16.44 (–)	9.72 (15.59)	8.25 (11.46)	0.00 (–)	0.00 (–)	0.00 (–)
Evergreen tree leaves	–	0.00 (–)	0.03 (0.09)	–	–	–	0.00 (–)	0.00 (–)	0.12 (0.13)	0.43 (–)	0.15 (0.27)	25.48 (42.79)
Woody tissues (twigs, bark, and dead leaves)	–	31.03 (3.81)	20.08 (11.13)	–	–	–	68.72 (–)	35.04 (19.62)	42.28 (18.30)	67.03 (–)	7.45 (0.45)	36.29 (14.58)
Acorns	–	0.00 (–)	0.06 (0.17)	–	–	–	9.59 (–)	3.74 (5.39)	25.96 (30.35)	0.22 (–)	0.08 (0.13)	0.00 (–)
Others (e.g., conifer tree and fern leaves)	–	0.39 (0.13)	0.67 (0.78)	–	–	–	1.37 (–)	4.64 (2.39)	3.47 (3.19)	4.74 (–)	1.95 (2.18)	2.11 (2.87)

[a] Sample size

significant difference in the diet composition of sika deer between the springs of these 2 years (Kaneko et al. 2020), indicating that moderate dependency on canopy subsidies was a consistent pattern in the spring diet composition of sika deer regardless of years.

18.5 Nutritional Value of Sika Deer Rumen Contents

In Kaneko et al. (2020), the crude protein (CP) contents of the 126 rumen content samples were also analyzed. Protein is an important nutrient that affects the body condition of ruminants (Leader-Williams 1988). Therefore, evaluation of the CP content values of the sika deer diet would be helpful to understand the backgrounds of sustaining the high-density sika deer population in a heavily browsed habitat from a nutritional perspective.

The CP content values of the sika deer rumen contents were high in the spring (Fig. 18.4). Robbins (1993) reviewed experimental feeding studies on white-tailed deer and roe deer (*Capreolus capreolus*) to derive the minimum dietary CP requirement estimates for wild ruminants. If we assumed the minimum dietary CP requirement estimates for maintenance to be 5–9% and those for maximum growth to be 13–20% based on this review, the CP content values of most spring samples were within the minimum dietary CP requirement estimates for maximum growth (Fig. 18.4). Japanese sika deer require a high amount of protein during spring season to improve their body condition that deteriorates during the previous winter season (Takatsuki 2006). The analysis of the CP contents revealed that the sika deer population in the Tanzawa Mountains could successfully obtain enough nutrition needed to improve their body condition from a mixture of little fresh greens and nearly unlimited canopy subsidies in the spring.

The CP content values seemed to be relatively stable among the summer, autumn, and winter samples (Fig. 18.4). None of the CP content values of the rumen content samples in these three seasons met the minimum dietary CP requirement estimates for maximum growth (Fig. 18.4). However, all CP content values were above the lower limit of the range of minimum dietary CP requirement estimates for maintenance (Fig. 18.4) even in autumn when the occupancy ratio of woody tissues (low-quality alternative resources) was the highest among the four seasons (Table 18.1). One possible explanation for this is that acorns may have contributed, to some extent, to obtain nutrition during the autumn season.

18.6 Body Condition of Fawns in Winter

In the Tanzawa Mountains, body mass (non-eviscerated weight) and hindfoot length (length from the top of the calcaneum to the tip of the hoof) of culled fawns (less than 1 year old) have been recorded by hunters according to the management plan.

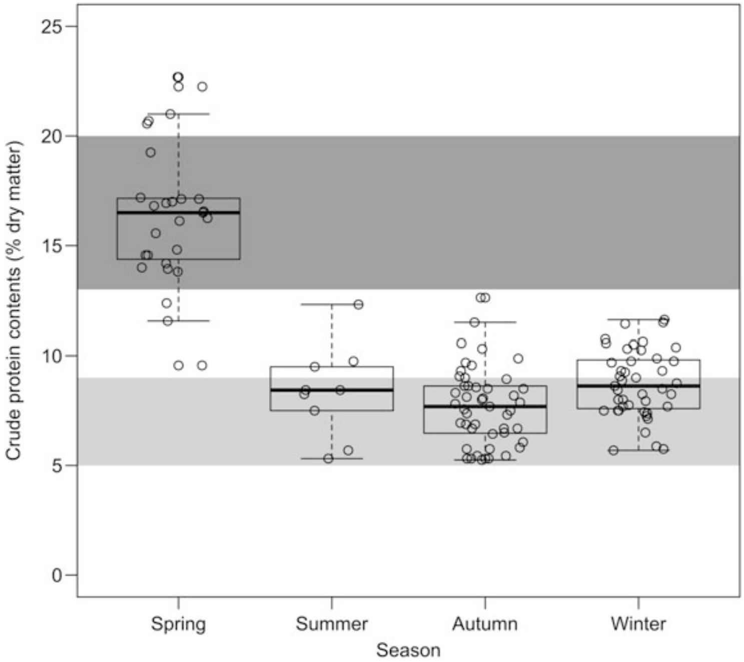

Fig. 18.4 Boxplot of the crude protein (CP) content values of the rumen contents of a sika deer population in the Tanzawa Mountains. The black bold lines in the boxes indicate the median CP content values for each season. Light and dark gray shaded areas indicate the ranges of the minimum dietary CP requirement estimates for maintenance (5–9%) and maximum growth (13–20%), respectively. The original data was from Kaneko et al. (2020)

Monitoring such deer body condition indicators enable us to evaluate the present state of the sika deer population and the potential of population growth. For example, body mass is largely related to overwintering survival rate (White and Bartmann 1998) and age at first reproduction (Kaji et al. 2009), which are critical demographic parameters that determine deer population growth rates.

In the area, the winter body mass of fawns (December to March) increased almost linearly, at least until FY2011 (Takeshita et al. 2019; Fig. 18.5). This result would reflect the decrease in deer density in the Tanzawa Mountains. Winter body mass of fawns in the Tanzawa Mountains recovered to 25–30 kg by FY2011; it was the similar level with another Japanese sika deer population that lived in habitats relatively less deteriorated compared with the Tanzawa Mountains (a sika deer population in Hyogo Prefecture; Yokoyama 2009).

In contrast to the winter body mass of fawns, there was no statistically significant increasing or decreasing trend in winter hindfoot length (Takeshita et al. 2019; Fig. 18.6). However, the length of the winter hindfoot of fawns in the Tanzawa Mountains in the first year of the management plan (i.e., FY2003) were relatively small compared with that in FY2004–2014; the length of the mean winter hindfoot of female and male fawns in FY2003 was 34.9 and 35.7 cm, respectively (Kanagawa

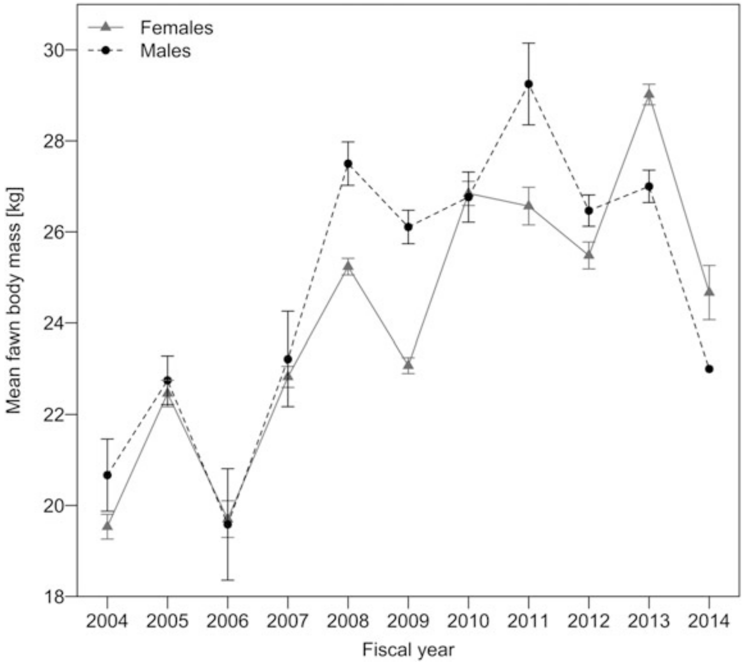

Fig. 18.5 Change in mean body mass of female and male (light-gray triangles with solid line and black circles with dashed line, respectively) sika deer fawns in the Tanzawa Mountains, during fiscal year (FY) 2004–2014 (from February 2005 to March 2015). The start of the FY in Japan is April; therefore, the winter FY2014 corresponds to the period ranging from December 2014 to March 2015 (note that the period of winter slightly differed from that in Kaneko et al. (2020) for practical reasons). Bars indicate the standard errors of the means. The original data was from Takeshita et al. (2019)

Prefecture unpublished data). Therefore, we suspect that hindfoot length may have a narrower range of change relative to other sika deer body measurements related to muscle and fat such as body mass and that the hindfoot length of fawns may have already recovered and reached nearly maximum by FY2004. Indeed, the winter hindfoot length of fawns in the Tanzawa Mountains in FY2004–2014 did not largely differ from that of the sika deer population in Hyogo Prefecture (Yokoyama 2009).

18.7 Canopy Subsidies as a Factor Sustaining the High-Density Sika Deer Population

In this chapter, we reviewed the population density, food habits, and body condition of the sika deer population in the Tanzawa Mountains, where understory vegetation has deteriorated excessively owing to the browsing pressure by sika deer. Sika deer

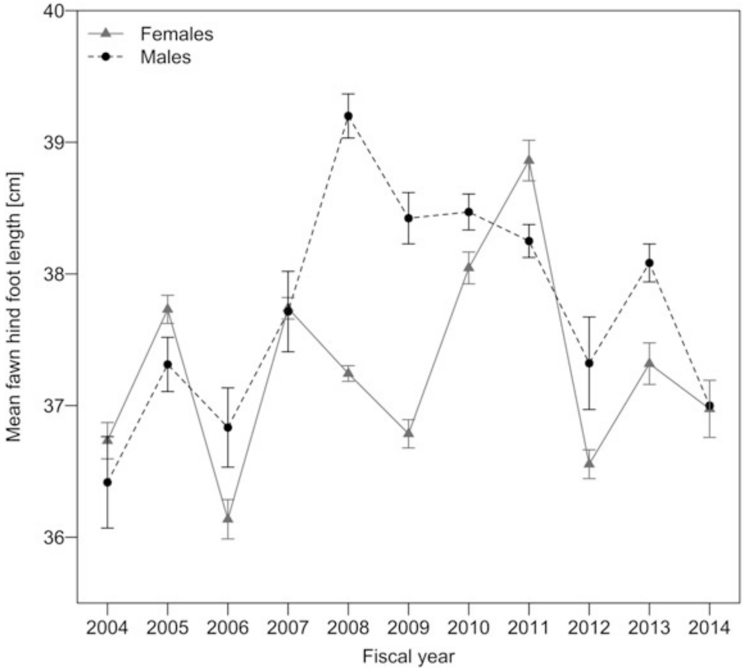

Fig. 18.6 Change in mean hindfoot length of female and male (light-gray triangles with solid line and black circles with dashed line, respectively) sika deer fawns in the Tanzawa Mountains, during fiscal year 2004–2014 (from February 2005 to March 2015). The start of the FY in Japan is April; therefore, the winter FY2014 corresponds to the period ranging from December 2014 to March 2015 (note that the period of winter slightly differed from that in Kaneko et al. (2020) for practical reasons). Bars indicate the standard errors of the means. The original data was from Takeshita et al. (2019)

forage various canopy subsidies throughout the year in a heavily browsed habitat. In general, deer overbrowsing leads to a reduction in the quality and quantity of food resources available to deer; thus, deer abundance will be expected to decline and settle in an equilibrium state around the lowered carrying capacity (Caughley 1970). However, if deer populations start to forage canopy subsidies, a natural regulation in the relationship between deer populations and their habitats will not be expected due to lacking immediate adverse feedback effects on deer population growth through limiting resources (i.e., lack of prompt herbivory-induced decreases in their annual production) (Kaji et al. 2009; Takeshita et al. 2018). Although we do not have quantitative data on the availability of tree leaves within the Tanzawa Mountains, we speculate that the tree leaf quantities in the relatively large forest area occupying approximately 70% of the Tanzawa Mountains would be enough to sustain the high-density sika deer population as shown in Nakanoshima Island, Lake Toya (Miyaki and Kaji 2004).

An analysis of the sika deer rumen contents revealed that the studied sika deer population could succeed in obtaining enough nutrition from a mixture of limited high-quality greens and nearly unlimited low-quality canopy subsidies. By utilizing large canopy subsidies, the sika deer population could increase their body condition even under a deteriorated habitat condition, where the culling program were progressed. In such a situation, unless more intensive culling programs are implemented, the sika deer population will increase again, and the habitat condition may further deteriorate owing to the continuous browsing pressure by sika deer. For the white-tailed deer population, improvements in deer demographic parameters related to mitigated density-dependent resource limitation were proposed as one reason for the unexpected increases in deer population following implementation of culling programs (Giles and Findlay 2004; Simard et al. 2013). Canopy subsidies are ubiquitous food resources in forest areas all over Japan. Therefore, to effectively conserve and promote restoration of sika deer habitats in Japan, long-term lethal control measures and the establishment of deer exclosure fences should be jointly implemented (also see Chaps. 26 and 33).

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Chapter 19
Effects of Sika Deer and the Unique Relationship with Forest Vegetation in Yakushima Island

Ryosuke Koda

Abstract Sika deer impacts on ecosystems have been well-studied in cool-temperate deciduous and coniferous forests, but those in evergreen broad-leaved forests are relatively unclear. Additionally, in exclosure experiments, which is the most commonly used approach, it has been difficult to observe the degradation of forest vegetation with an increase in deer density by comparing multiple density levels. On Yakushima Island, southwestern Japan, large undisturbed evergreen broad-leaved forests can be found to analyze deer effects by comparing temporal and spatial heterogeneities in deer density. Several studies have revealed that vegetation in evergreen broad-leaved forest were affected by increasing sika deer on Yakushima Island, and sika deer can have similar effects on forest ecosystems throughout their distribution range. On the other hand, it is also suggested that the impact on the forest regeneration may be relatively suppressed as compared with deer population density, which may be attributable to the characteristic morphology of the endemic sika deer, high productivity in evergreen broad-leaved forests, and the unique relationship between deer and forest vegetation. For better insights on the function of deer as a driver of community dynamics of forest vegetation, it is important to investigate the relationships between deer density and forest vegetation in diverse deer–forest systems.

19.1 Introduction

Increasing sika deer (*Cervus nippon*) populations can have considerable effects on forest vegetation, which has been investigated in many studies (Takatsuki 1989, 2009). Nonetheless, most studies have been conducted in cool-temperate deciduous and coniferous forests. Therefore, how the impacts of sika deer vary throughout their distribution range, especially in evergreen broad-leaved forests, is still unclear.

R. Koda (✉)
Biodiversity Research Center, Research Institute of Environment, Agriculture and Fisheries, Osaka Prefecture, Neyagawa, Japan
e-mail: KoudaR@mbox.kannousuiken-osaka.or.jp

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In addition, there are certain biases in previous studies owing to the experimental approaches. Field experiments using fences (exclosures) to exclude deer are the most common approach that has been conducted for several deer species (Gordon et al. 2004; Hester et al. 2000). Exclosure experiments can clearly demonstrate the impacts of deer in a region by comparing "no deer" and "high-density deer" populations (Takatsuki 2009). In exclosure experiments, however, it is difficult to establish multiple levels of deer density (Rooney and Waller 2003; Suzuki et al. 2008; but see Horsley et al. 2003 as an exception), which makes it difficult to observe the degradation process of forest vegetation with increasing deer density (Rooney and Waller 2003). Therefore, to explain the relationship between deer and forest vegetation, it is necessary to compare the effects of deer at various densities using approaches other than enclosure experiments.

In Japan, one of the largest, relatively undisturbed, evergreen broad-leaved forest exists on Yakushima Island (Kohyama and Aiba 1997); an endemic subspecies of the Japanese sika deer, *Cervus nippon yakushimae*, is predominantly found here (Kagoshimaken Sizenaigo Kyokai 1981), with a widely varying population density among different areas on the island (Agetsuma et al. 2016). In the western area of the island, several studies on forest vegetation have been conducted before the 1990s (e.g., Aiba and Kohyama 1996, 1997; Tagawa 1980); however, the population size of the deer has witnessed a monumental increase since then (Agetsuma et al. 2003; Tsujino et al. 2004; Tsujino and Yumoto 2004). Therefore, it is possible to analyze the effects of deer on the vegetation of evergreen broad-leaved forests on Yakushima Island, by comparing temporal and spatial heterogeneities in deer density.

The aim of this chapter is to assess the effects of deer in evergreen broad-leaved forests and the relationship between an increasing deer density and forest vegetation. First, from long-term monitoring data, the effects of increasing deer density on tree saplings were identified. Later, from comparisons across spatial heterogeneity, relationships among deer density, deer feeding pressure, and plant species richness and coverage were examined. Finally, on comparing these relationships among different types of forest management (primary, secondary, and plantation forests), the unique relationship of sika deer with forest vegetation in the evergreen broad-leaved forests on Yakushima Island are discussed.

19.2 Environment and Sika Deer in Yakushima Island

Yakushima Island (approximately 500 km^2) is a mountainous island composed predominantly of granite and is located approximately 70 km south of Kyushu, Japan (30° 20′N, 131° 30′E, Fig. 19.1), with the highest peak reaching 1936 m a.s.l. The average annual rainfall ranges from 2400 to 5000 mm along the coast and exceeds 7000 mm in some inland mountainous areas (Takahara and Matsumoto 2002). Primary forests at altitudes less than 800 m a.s.l. are warm-temperate evergreen broad-leaved forests (Aiba et al. 2001), mainly consisting of Fagaceae, Hamamelidaceae, Myrsinaceae, and Lauraceae (Agetsuma 1995; Tsujino et al.

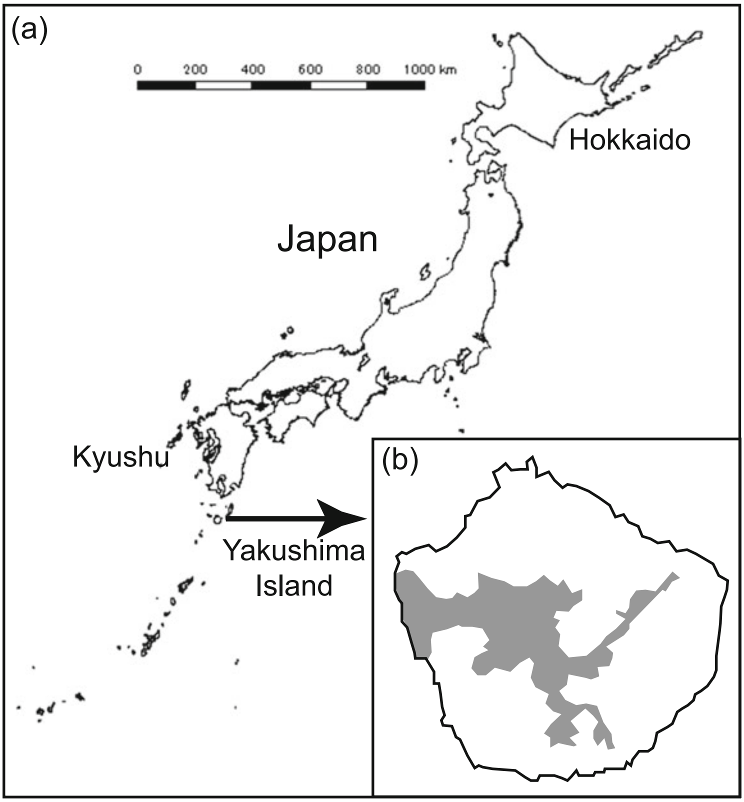

Fig. 19.1 Location of (**a**) Yakushima Island in Japan and (**b**) Natural World Heritage area in Yakushima Island (gray area)

2006). Since the last 50 years, large areas of primary forests at lower altitudes have been clear-felled (Agetsuma 2007), and most of the clear-felled land has been converted to conifer plantations of sugi-cedar (*Cryptomeria japonica*) (Aiba et al. 2001). However, secondary stands of evergreen broad-leaved forests have regenerated naturally (Aiba et al. 2001), and large undisturbed broad-leaved forests are still present. Owing to its important value, the nature on Yakushima Island was partly designated as a Natural World Heritage by the UNESCO in 1993 (Fig. 19.1).

A subspecies of Japanese sika deer, *C. n. yakushimae*, is endemic to Yakushima Island and to Kuchinoerabujima Island, a small volcanic island 12 km northwest of Yakushima. The body weights of adult males and females of *C. n. yakushimae* are 24–37 kg and 19–25 kg, respectively (N. Agetsuma, unpublished data), and these weights are lower than those of other *C. nippon* subspecies (Takatsuki 2006). Additionally, *C. n. yakushimae* has a short-legged morphology adapted to the steep terrain of Yakushima Island (Terada et al. 2012). Reflecting on these morphological characteristics, the feeding height of *C. n. yakushimae* is relatively low at approximately 130 cm (Koda and Fujita 2011). In broad-leaved forests, deer mainly

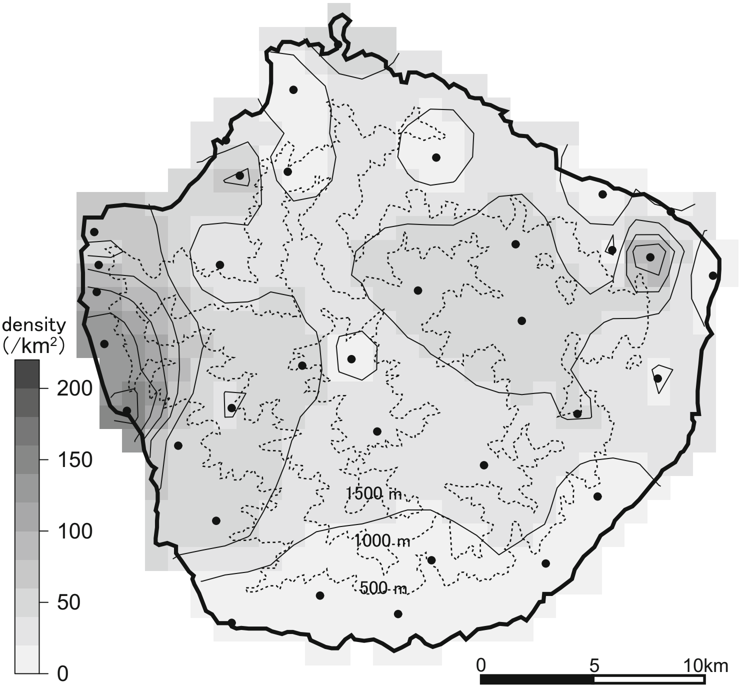

Fig. 19.2 Estimated distribution of deer population density around 2008 using the inverse distance weighting (IDW) method. Dots indicate study sites for density estimation

feed on broad leaves and can be classified as browsers (Agetsuma et al. 2011), whereas in coniferous forests and dwarf bamboo grasslands at high altitudes, they largely depend on graminoids (Takatsuki 1990). The home ranges of deer in Yakushima Island are rather small, especially for adult females (7–17 ha; adult males: 4–78 ha) and are mostly constant in all seasons (see Agetsuma et al. 2016). On Yakushima Island, large mammals are limited to deer and Yakushima macaques (*Macaca fuscata yakui*). Natural predators have never existed, and natural forests and native deer have coexisted for eons (Agetsuma et al. 2003).

The population density of deer varies greatly across regions in the islands. Figure 19.2 shows the estimated distribution of deer population density around 2008 using the inverse distance weighting (IDW) method. The deer population density was estimated at 35 sites (Koda and Fujita 2011; Koda and Kawamura 2012; Koda et al. unpublished data) using the fecal accumulation rate technique (Koda et al. 2011). Deer density was high in the western region and part of the eastern region but low in the southern region. The total population size was estimated to be approximately 17,000 in 2008. The reasons for different deer densities among the areas are still unclear, but differences in hunting and culling pressure (mainly as pest control around farmlands) and habitat degradation may have affected the deer distribution pattern. According to camera trap data, deer population density

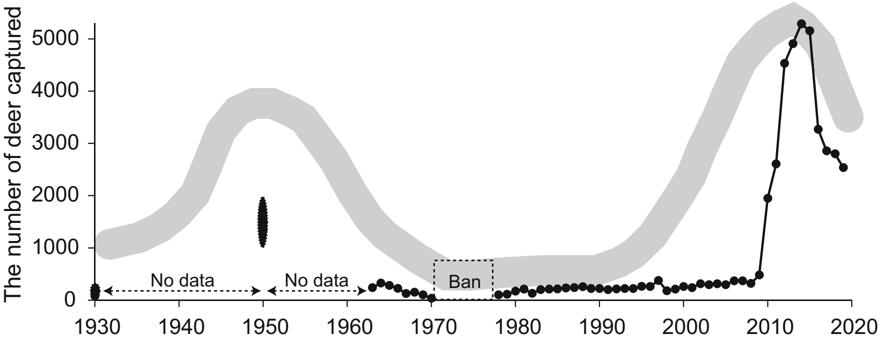

Fig. 19.3 Changes in the number of deer captured on Yakushima Island over the last 90 years according to Tsujino (2014), Fujimaki et al. (2016), and Kagoshima Prefecture (2020b). Plots in 1930 and 1950 indicate the range of deer caught according to Shirai (1956). The thick gray curve indicates the trends in deer population according to Tsujino (2014) and Kagoshima Prefecture (2020a)

tends to be high in evergreen broad-leaved forests and grassland areas, and low in coniferous forests and agricultural lands (Agetsuma et al. 2016).

The deer population size and hunting pressure have changed dramatically over the last 90 years (Fig. 19.3). Deer hunting was traditionally conducted, and more than 1000 deer could be hunted per year during the 1950s (Shirai 1956). However, deer hunting has been banned since 1970 due to a decreasing deer population (Agetsuma 2007). Since 1978, pest control restarted only around farmlands, and the number of deer culled per year has remained at 200–300 (Agetsuma 2007). Since 2010, however, the number of culled deer has increased rapidly; it was over 5000 in 2014 (Fig. 19.3). Consequently, the deer population size in 2019 is estimated to be around 10,000 (Kagoshima Prefecture 2020a).

19.3 Long-Term Changes in Sapling Vegetation

Long-term monitoring of deer populations and forest vegetation was carried out in a natural world heritage area on the western part of Yakushima Island. For deer population monitoring, roadside counts of deer on a 1.2 km route were conducted between 1988 and 2006 (Koda et al. 2008; Tsujino et al. 2004). Encounter rates of deer were calculated as the number of deer seen per kilometer and were compared among the years. In addition, deer population densities since 2000 have been estimated in several studies (Agetsuma et al. 2003; Koda et al. 2011; Tsujino and Yumoto 2004). Over 18 years, the encounter rate of deer continued to increase, suggesting a continuous increase in deer density in this area. The estimated deer density was reported to be 50–80 deer/km^2 around 2000 (Agetsuma et al. 2003; Tsujino and Yumoto 2004), which increased to 96–112 deer/km^2 in 2007 and 2008

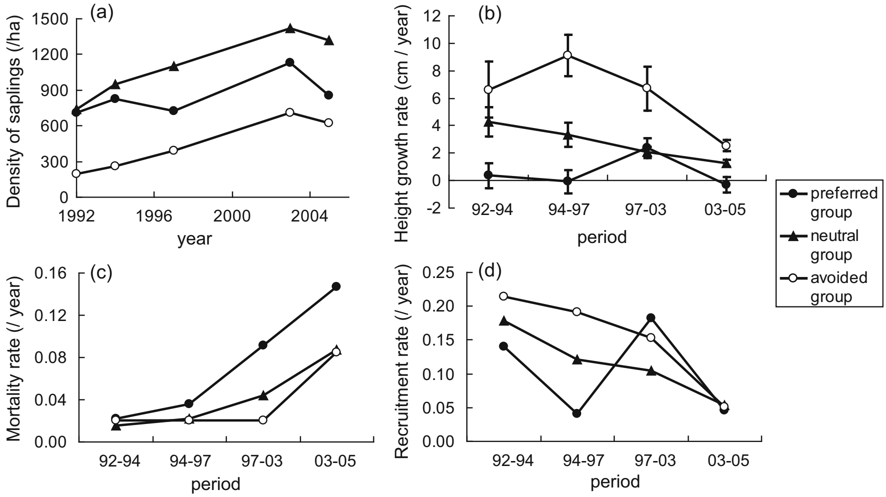

Fig. 19.4 Changes of sapling vegetation in each preference group divided into preferred, neutral (neither preferred nor avoided), and avoided group based on the feeding frequency (i.e., the number of saplings with browsing scars caused by deer per total number of saplings). (**a**) Densities (/ha), (**b**) mean growth rates (cm/year), (**c**) mortality rates (/year), and (**d**) recruitment rates (/year). Error bars indicate standard error of the mean

(Koda et al. 2011). Thus, the population size of deer increased after the 1990s and became exceedingly high in this area.

Tree saplings have been affected under continuous deer population growth (Koda et al. 2008). Fig. 19.4 shows the changes in densities, mean growth rate, mortality rate, and recruitment rate of 50–130 cm in height tree saplings on 0.13 ha between 1992 and 2005. Tree sapling species were divided into three groups: preferred, neutral (neither preferred nor avoided), and avoided group based on the feeding frequency (i.e., the number of saplings with browsing scars caused by deer per total number of saplings). The preferred group continuously had a low growth rate, while their mortality rate increased over time, which suggested that increasing deer density can result in increasing feeding pressure that first affects growth and later affects sapling mortality. In addition, the growth rates of the neutral and avoided groups decreased over time, while their mortality rates increased. Clearly, even in the evergreen broad-leaved forest on Yakushima Island, direct feeding pressures and indirect physical effects by increasing deer density affect the growth and mortality of tree saplings, and this may be true for other forests in Japan as well.

On the other hand, tree sapling density has been well maintained with increasing deer density in this forest. Sapling density did not decrease with increasing deer density, even for the preferred group probably due to the high recruitment rate between 1997 and 2003 (Fig. 19.4a, d). The factor of this high recruitment rate is unclear, but it is suggested that root-sprouting shoots of *Myrsine seguinii*, a preferred species, may have increased (Koda et al. 2008). In this forest, Tsujino and Yumoto (2004) surveyed tree seedlings less than 50 cm in height in 2002, and Koda and

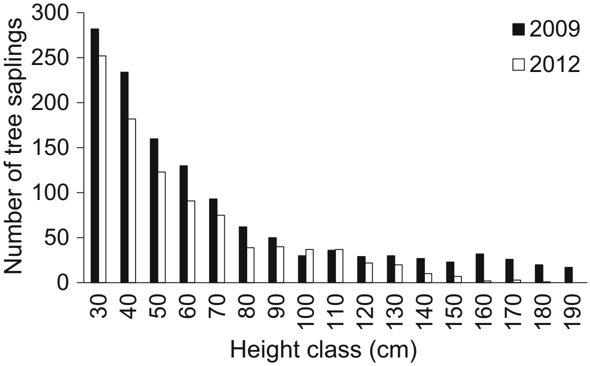

Fig. 19.5 Histogram of tree saplings in 2009 and 2012 on the same 40 m × 60 m plot

Fujita (2011) surveyed tree saplings over 30 cm in height in the same area in 2009. They reported that the histogram of tree seedlings and saplings showed a typical reverse J-shape, suggesting that many small trees could be found. Although the number of saplings had decreased slightly, many still remained, and the histogram showed a similar shape in 2012 (R. Koda, unpublished data; Fig. 19.5). Moreover, Agetsuma and Agetsuma-Yanagihara (2018) reported that natural vegetation gradually recovered after a mudslide in this area under 90.9–206.9 deer/km^2 between 2012 and 2017 (Kagoshima Prefecture 2020a). For the Japanese sika deer, it has been reported that 17.5–30.9 deer/km^2 in Mt. Ohdaigahara, central Japan (Maeji et al. 1999); 22.4–37.9 deer/km^2 in Boso Peninsula, central Japan (Asada and Ochiai 1996); and about 60 deer/km^2 in Kinkazan Island, northern Japan (Takatsuki and Gorai 1994), affect forest vegetation and regeneration by browsing and bark stripping. These deer densities are either similar to or lower than the deer densities estimated in this area. Thus, in the evergreen broad-leaved forest on Yakushima Island, deer impacts on forest vegetation are relatively low compared to the deer population density.

19.4 Relationship Between Deer Density and Deer Feeding Pressure

The intensity of deer feeding pressure has been assumed to be directly proportional to their population size. Deer impacts on forest vegetation are mostly discussed based on these assumptions (reviews in Gill 1992; Côté et al. 2004; Takatsuki 2009). However, nonlinear relationships between deer population density and impacts on forest vegetation have also been suggested (Hester et al. 2000; Suzuki et al. 2008; Tremblay et al. 2006). To assess the relationship between deer population density and deer impact on forest vegetation, deer population density and tree sapling vegetation were surveyed in six evergreen broad-leaved forests with different deer densities on Yakushima Island (Koda and Fujita 2011). As an index of deer feeding

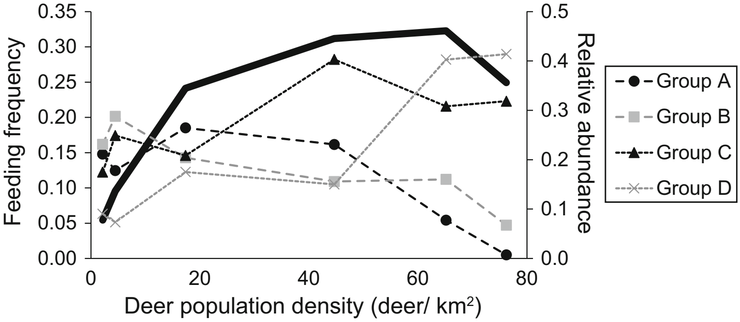

Fig. 19.6 Relationships of deer density with the feeding frequency of tree saplings (black thick line) and relative abundance of sapling species in each preference group. Feeding frequencies were calculated as the number of individuals having browsing scars caused by deer per total number of individuals. Based on the feeding frequency of each sapling species and deer density in each site, tree sapling species were divided into four preference groups, groups A–D. Group A may include the most palatable species, while group D may include the least palatable species. The relative abundance of a group was calculated as the number of individuals in that group per total number of individuals

pressure, feeding frequency of tree saplings 30–130 in height (i.e., the number of individuals having browsing scars caused by deer per total number of individuals) were calculated. The feeding frequency and browsing rate have often been used to assess the intensity of deer herbivory (e.g., Crimmins et al. 2010; Miller et al. 2009). In addition, based on the feeding frequency of each sapling species and deer density in each site, tree sapling species were divided into four preference groups, groups A–D, and relative abundances of each group were compared (Koda and Fujita 2011). Here, group A may include the most palatable species for deer, while group D may include the least palatable species. The relative abundance of a group in each site was calculated as the number of individuals in that group per total number of individuals in that site.

After a certain level, the deer population density did not contribute to an increase in the feeding frequency (Fig. 19.6). In areas with a deer density lower than 20 deer/km^2, the feeding frequency increased with deer density. However, areas with deer densities higher than 20 deer/km^2 showed similar feeding frequency values (0.24–0.32). Relative abundances of groups A and B decreased and became rare, while those of groups C and D increased with increasing deer density (Fig. 19.6). Although sapling species of group D were rarely fed and classified as avoided species in deer-abundant area, most sapling species of group C were relatively fed and classified as preferred species in same area (Koda and Fujita 2011). These data suggest that deer left many available saplings without feeding and shifted their main food items to other foods in deer-abundant area. Deer can alter their feeding behavior depending on the change in the availability of their forages (Johnson et al. 1995). Agetsuma et al. (2011) observed deer foraging behavior in deer-abundant areas (>80 deer/km^2) and reported that 75% of the deer diet consisted of forest litter, such as fallen leaves, flowers, or fruits, even though deer had access to abundant living edible leaves in the study area. Thus, it seems likely that the dependence on litterfall as the diet increased along with increasing deer density in the forests with deer densities higher than 20 deer/km^2, which resulted in a nonlinear relationship between deer density and deer feeding pressure. The preference of litterfall is probably lower than fresh leaves of groups A and B but higher than those of group C, which may increase dependence on litterfall in deer-abundant area where groups A and B decrease. Clearly, the relationship between deer density and deer feeding pressure on forest vegetation can become nonlinear due to a shift of the food, and this nonlinear relationship can change the intensity of deer impacts.

19.5 Responses of Forest Floor Vegetation to Deer Density Increase and Differences among Forest Management Types

Under the nonlinear relationship between deer density and deer feeding pressure, how do plant species richness and coverage on the forest floor respond to increasing deer density? To test the relationships between deer density and forest vegetation, 488 study plots (10 m × 4 m) were established in lowland primary, secondary, and plantation forests on Yakushima Island. In each study plot, estimates of deer density; surveys of forest floor vegetation, including trees, shrubs, herbs, lianas, and ferns; and surveys of several environmental factors such as light condition, angle of slope, topographic position, and mean annual rainfall were conducted (Koda et al. unpublished data). To test the possible nonlinear relationship, generalized additive mixed model (GAMM) analyses were used for each forest type (primary, secondary, and plantation).

The relationships among deer density, plant species richness, and total coverage of forest floor vegetation differed among forest types. In the primary forest, the number of plant species showed a nonlinear relationship with deer density (Fig. 19.7a). Along with an increase in deer density, the number of plant species increased, reached a maximum at approximately 20 deer/km^2, and thereafter decreased. In primary forests, relative abundances of highly preferred species decreased with increasing deer density, those of some moderately preferred species showed peaks at intermediate deer density levels, while those of some avoided species increased with increasing deer density (Koda and Fujita 2011; Koda et al. unpublished data). Thus, changes in plant species composition depending on deer food preferences and plant traits maximize plant species richness under intermediate deer density. For total coverage of forest floor vegetation in the primary forest, deer density showed a negative linear relationship (Fig. 19.7b). This result is consistent with previous studies that compared multiple levels of deer density (Gill and Morgan 2010; Tremblay et al. 2006, 2007), suggesting deer impacts on the plant biomass of forest vegetation. On the other hand, tree sapling vegetation was well maintained under increasing deer density on the western primary forest in Yakushima Island

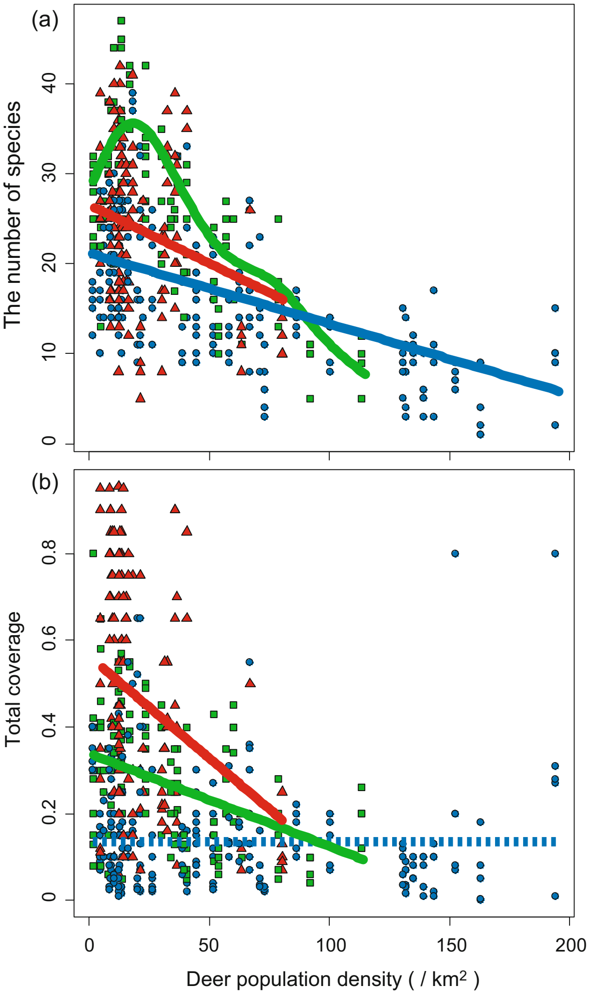

Fig. 19.7 Relationships of deer density with (**a**) the number of plant species and (**b**) total coverage of forest floor vegetation. Green square, blue circle, and red triangle indicate the data in each plot on primary, secondary, and plantation forests, respectively. Green, blue, and red lines indicate the predicted relationship in primary, secondary, and plantation forests, respectively. Dashed line indicates the mean value as deer density was not a selected factor in the predicted model

(Koda et al. 2008). These data suggest that forest floor vegetation such as herbs and ferns rather than tree saplings is vulnerable to deer impacts, which may result in linear decrease with increasing deer density. Clearly, even in the evergreen primary forest on Yakushima Island, increasing deer density can affect plant species composition and plant biomass on forest floor vegetation.

In secondary and plantation forests, plant species richness decreased linearly with an increase in deer density and was not maximized at intermediate deer densities (Fig. 19.7a). In addition, the coverage in secondary forests did not show a significant relationship with deer density and was minimal even in deer-scarce areas (Fig. 19.7b). In plantation forests in Yakushima Island, large areas of forest floor are often covered with fern species (Terada et al. 2010), such as *Nephrolepis auriculata*, *Gleichenia japonica*, *Microlepia strigosa*, and *Dicranopteris dichotoma*

(Koda et al. unpublished data); their coverage linearly decreased with increasing deer density. One of the largest differences among forest types is logging history. In Yakushima Island, most secondary and plantation forests have been clear-felled by mechanized methods for firewood, timber, and pulp production over the past 50 years (Agetsuma 2007; Aiba et al. 2001; Otani et al. 2007). Logging for forest management has considerable effects on forest floor vegetation (Hedwall et al. 2013; Kenderes and Standovár 2003) through changes in light conditions (Murcia 1995). Therefore, it is possible that the abundance of many plant species may be suppressed due to changes in the light condition, which results in the linear decrease of plant species richness with increasing deer density and a low coverage independent of the deer density in secondary forests. Additionally, a high abundance of ferns in plantation forests may suppress the appearance of many species, resulting in the linear decrease without a maximal peak of plant species richness. Clearly, forest management markedly affects plant species composition and abundance (Bhuju and Ohsawa 1999; Nagaike 2002), which in turn alters the relationship between deer density and forest vegetation. Therefore, it is important to note the history of forest management while discussing the impact of deer on forest vegetation.

19.6 Conclusion

Even in the evergreen broad-leaved forest on Yakushima Island, several impacts of sika deer on forest vegetation are detected. For example, the growth and mortality of tree saplings were affected (Fig. 19.4b, c), the composition of tree saplings changed with increasing deer density (Fig. 19.6), and the plant species richness and the total coverage of forest floor vegetation decreased with increasing deer density (Fig. 19.7). These results are consistent with several studies which have been conducted in other forests such as cool-temperate deciduous and coniferous forests (reviews in Takatsuki 1989, 2009), suggesting that sika deer can have similar effects on forest ecosystems throughout their distribution range.

On the other hand, some results, especially those related to tree saplings, suggest that the effects of sika deer on the forest regeneration may be relatively suppressed as compared with deer population density on Yakushima Island. For example, tree sapling density was well maintained with increasing deer density (Fig. 19.4a), and the histogram of tree saplings showed a typical reverse J-shape (Fig. 19.5) under high density of deer (>80 deer/km^2). Three factors have been suggested that allow deer to constantly persist at high densities without causing serious damage to the forest regeneration on Yakushima Island (Agetsuma et al. 2003). These factors are as follows: (1) *C. n. yakushimae* has the smallest in size among all *C. nippon* subspecies; (2) evergreen forests have a higher carrying capacity than deciduous forests, especially in winter; and (3) natural forests and native sika deer have coexisted without predators and significant disturbances since the Ice Age. The short-legged morphology of *C. n. yakushimae* (Terada et al. 2012) and factor (1) may result in a lower browsing height (Koda and Fujita 2011), which protects the growing saplings from the feeding pressure of the deer. The constant home range in all seasons (Agetsuma et al. 2016) is related to factor (2), which suggests that food resources for deer are stable and sufficient throughout the year. In addition, the nonlinear relationship between deer density and deer feeding pressure (Koda and Fujita 2011), probably resulting from a high dependence on forest litter than other living edible leaves as diet (Agetsuma et al. 2011), is related to factor (3), suggesting that *C. n. yakushimae* might have an ecological trait such as flexible food selection including litterfall, which may consequently suppress the impact on forest vegetation. Although most fern species are typically considered as avoided species (Rooney and Waller 2003), *C. n. yakushimae* prefer many fern species, such as *Angiopteris lygodiifolia*, *Lindsaea* spp., and *Diplazium* spp. (data not shown). These wide preferences for food are also related to factor (3). However, it is important to note that damage to the forest regeneration could arise in the future. Agetsuma et al. (2021) reported that deer on the western part of Yakushima Island continued to increase and began to decrease in 2014. These changes suggest that deer in this area may have reached carrying capacity. Decrease in sapling density between 2009 and 2012 in this area (Fig. 19.5) may indicate increasing impacts of deer on tree saplings. In addition, relationship between deer density and forest vegetation can be altered by several factors such as forest management history (Fig. 19.7). Therefore, it is important to continue monitoring these forest communities to preserve the unique ecosystem on Yakushima Island.

Site characteristics, such as differences in vegetation composition and environmental conditions, can affect deer impacts on forest vegetation (Gill and Beardall 2001). Most previous studies have been conducted in cool-temperate deciduous and/or coniferous forests (Agetsuma et al. 2003). In cool-temperate forests, plant productivity and plant species richness are different from those in evergreen broad-leaved forests. Therefore, it is possible that the vegetation in cool-temperate forests responds to increasing deer density, unlike the results in evergreen broad-leaved forests shown in this chapter. For better understanding the functions of deer as a driving force of community dynamics of forest vegetation, it is important to investigate the relationships between deer density and forest vegetation in diverse deer-forest systems and to compare these relationships and mechanisms with those on Yakushima Island.

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Part IV
Impact on Ecosystem and Its Resilience

Chapter 20
Conserving the Plant Community and Its Resilience Using Deer-Proof Fences in Japan

Yushin Shinoda, Hiroyuki Uno, and Munemitsu Akasaka

Abstract To protect and/or restore plants from deer grazing, deer-proof fence is considered as a key tool, together with deer population management through culling. However, installation and maintenance of large-scale fences are generally impractical in Japan, because of steep and complex terrain, heavy snows, and frequently natural disaster. Even if each size of fence is limited, fences are effective for plant conservation when locations to install the fences are well targeted. In particular, protection of vulnerable species and seeds in seed bank by deer-proof fence could be effective even if small-sized fence can be installed, because they could disappear from focal area/region before population management successes. In this chapter, we overviewed distribution of the size of installed fences and purpose of the installation in Japan and provided clues to prioritize conservation targets and actions along the deer grazing severity gradient. For efficient conservation through fence installation, prioritization targets to be conserved need to be set carefully.

20.1 The Need to Conserve Plants with Deer-Proof Fences

Widespread impacts of deer grazing on plant populations have been observed throughout the northern hemisphere due to climate change, decreases in predators and hunters, and human introductions (Côté et al. 2004; Takatsuki 2009). Deer grazing continuously disrupts plant reproduction, strongly impacting plant survival and resilience (Côté et al. 2004; Takatsuki 2009). Additionally, deer grazing indirectly impacts various taxa (e.g., small mammals, birds, and insects) and abiotic

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Y. Shinoda (✉)
Institute of Agriculture, Tokyo University of Agriculture and Technology, Fuchu, Japan

Present address: Center for Environmental Biology and Ecosystem Studies, National Institute for Environmental Studies, Tsukuba, Japan
e-mail: yushin0423@yahoo.co.jp

H. Uno · M. Akasaka
Faculty of Agriculture, Tokyo University of Agriculture and Technology, Fuchu, Japan
e-mail: unoh@go.tuat.ac.jp; muuak@cc.tuat.ac.jp

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conditions (e.g., soil nutrients and moisture) by reducing the abundance of particular plant species and vegetative cover (Gass and Binkley 2011; Cournane et al. 2011; DiTommaso et al. 2014; Iida et al. 2016). In recent decades, deer-proof fences, together with deer population management through culling (Takatsuki 2009; Royo et al. 2010; Wright et al. 2012; Takeshita et al. 2016), have been used to protect and/or restore plants from deer grazing (Lemieux et al. 2000; Takatsuki 2009; Royo et al. 2010; Wright et al. 2012; Nagaike et al. 2014; Nuttle et al. 2014; Uno et al. 2019). Although plant communities fully recover after fence installation in some cases (Kumar et al. 2006; Abrams and Johnson 2012; Inatomi et al. 2012; Nagaike et al. 2014; Wilbur et al. 2017), in others, plant species do not recover from deer grazing, even after substantial time has elapsed (Royo et al. 2010; Nuttle et al. 2014; Shinoda and Akasaka 2019; Chap. 33). Such mixed findings have ignited discussions on the mechanisms behind the slow or unsuccessful vegetation recovery after fence installation (Gass and Binkley 2011; Nuttle et al. 2014; Ramsey et al. 2017). Seven processes that contribute to the success and speed of vegetation recovery from deer grazing were summarized by Tanentzap et al. (2012):

1. Slow growth rates of plants relative to the plant biomass consumption by deer.

   Seedlings and saplings take years to mature. When planned deer culling is incomplete or fencing fails to exclude deer completely, the degree of understory vegetation recovery or seedling/sapling growth cannot compensate for the plants consumed by deer (Tanentzap et al. 2009; Ramsey et al. 2017).
2. Seed source depletion of deer-preferred plants.

   Deer grazing decreases and sometimes eliminates palatable plant species from a region. When palatable plant species are lost or reduced in abundance by deer grazing, the presence of propagule sources (i.e., soil seed banks) or seed dispersal from an external population is essential for plant recovery (González et al. 2010; Tamura 2016; Shinoda and Akasaka 2020; Shinoda et al. 2020). When deer grazing is not severe, plants can complement reductions in seed bank density by recruiting newly produced seeds. Conversely, when deer overgrazing persists in the long term, palatable plants cannot produce seeds due to the loss of their aboveground parts; thus, the seed bank density decreases continuously, which can result in the local extinction of the species (Miller et al. 2007; Shinoda and Akasaka 2019). Moreover, when deer overgrazing also prevails in surrounding regions, plant reproduction, and emigration from the surrounding regions are restricted (Buma and Wessman 2011; Tamura 2016). Due to these compounding factors, the recovery of palatable plants can be difficult, even when deer density decreases.
3. Alternative vegetation development under intense deer grazing.

   When unpalatable plant species or species tolerant to grazing become dominant in a vegetation patch under continuous deer overgrazing, the establishment of other plant species may be limited by competition for resources (e.g., space, amount, and quality of light, nutrients). The dominance of unpalatable or tolerant species may persist for long periods, preventing the recovery of other species even after deer density is reduced (Nuttle et al. 2014).

4. Preferential grazing on palatable species under low deer density.

   Deer will forage unpalatable species or even litters when palatable species are lost (Takahashi and Kaji 2001). Even if some palatable plant species begin to recover after deer density is reduced, their growth and recovery might be limited by selective foraging of palatable species by deer (Coomes et al. 2003).
5. Variation in grazing damage on palatable species within a plant community (e.g., associational resistance or susceptibility).

   The effects of deer grazing on plant communities are not the same within and among ecosystems. For example, the degree of change in a community caused by grazing could vary with the proportion of grazing-tolerant/competitive species in the community (Augustine and Frelich 1998; Côté et al. 2004). The probability and speed of vegetation recovery could also be influenced by the community composition before the presence of deer grazing.
6. Suppression of trophic cascades.

   Deer induce cascading effects on animal communities directly through resource competition and indirectly by modifying the physical environment (Côté et al. 2004). For example, excluding red deer (*Cervus elaphus* L.), roe deer (*Capreolus capreolus* L.), and mouflon (*Ovis ammon musimon* L.) increased density of mice, which predate plant seeds (Smit et al. 2001). Thereby, deer exclusion prevented recovery and regeneration of vegetation indirectly (Smit et al. 2001).
7. Changes in abiotic conditions associated with other ecological processes.

   The decline of vegetation caused by deer overgrazing decreases nitrogen and phosphorus contents in the soil through erosion and deterioration of litter decomposition via soil drying (Gass and Binkley 2011; Cournane et al. 2011). In other words, deer overgrazing can alter abiotic conditions (e.g., decrease soil nutrients and moisture), consequently delaying or restricting vegetation recovery. In addition, trampling pressure by deer hardens the soil surface and restricts plant recovery (Lemieux et al. 2000; Albon et al. 2007).

Among the seven conditions, seed source depletion is the most important for understanding and predicting the impacts of deer grazing on plant population dynamics because of the following reason. The loss of germinable seeds from the soil seed bank accompanied by the loss of aboveground plant parts results in a complete loss of the species from the region (i.e., local extinction) (Sletvold and Rydgren 2007; Enright et al. 2014; Manna et al. 2017). Thus, deer grazing can result in a genetic bottleneck and/or extinction of the plant population (Scheffer et al. 2001; Foley et al. 2003; Yan et al. 2009; Manna et al. 2017). Deer grazing decreases the source of plant resilience (e.g., seeds or propagules in soil that many plants rely on for aboveground recovery from disturbance), amplifying the impacts of subsequent disturbances (Scheffer et al. 2001; Enright et al. 2014; Ohashi and Hoshino 2014; Ingrisch and Bahn 2018). Although deer culling is a common practice for protecting plant populations and communities, the time lag between the initiation of culling and the effects of culling on plants is evident (Tanentzap et al. 2009; Takatsuki 2009; Wright et al. 2012). Conversely, deer-proof fence installation provides immediate protection to seed sources and seed banks, which can prevent genetic bottlenecks and/or local extinctions.

20.2 Current Status of Deer-Proof Fences

Many studies have examined the efficacy of fence installation for mitigating deer grazing impacts. Deer-proof fences are effective not only to protect plants but also to protect soil, agricultural products, and species in other taxa. In some cases, fences are installed to prevent soil erosion, soil nutrient loss, or soil drying caused by vegetation decline or the accumulation of deer feces (Mohr and Topp 2005; Risch et al. 2015). Fences are also used to protect crops and livestock from growth reductions—in farmlands and pastures, deer grazing and trampling damage crops and grass for livestock (Hildreth et al. 2012; Takayama et al. 2013; Johnson et al. 2014). Furthermore, fences are installed to prevent the indirect effects of deer grazing on species than plants (Holt et al. 2010; Rearick et al. 2011; Cocquelet et al. 2019). Deer grazing reduces vegetation cover, plant species diversity, and leaf, flower, and fruit quantities (Côté et al. 2004; Lin and Galloway 2010). These reductions subsequently diminish air and soil moisture, suitable nesting or breeding sites, and food for insects, birds, and earthworms (Holt et al. 2010; Rearick et al. 2011; Iida et al. 2016; Cocquelet et al. 2019; Nakahama et al. 2020).

In this chapter, we provide an overview of deer exclosure characteristics. Deer exclosures are defined as structures that exclude deer from a focal area by enclosing the area with a deer-proof fence. We conducted a search of peer-reviewed studies in Japan as well as a global systematic literature survey to investigate the size and purpose of deer-proof fence installations. We searched for scientific literature with the terms "deer" and "fence" using Google Scholar on 20 November 2020. We also searched J-stage (an electronic platform of journals written in Japanese, https://www.jstage.jst.go.jp/browse/-char/en) with relevant Japanese terms. From the results of these searches, we compiled a list of literature reporting the size, study region, and year of deer-proof fence system installation. We excluded studies where the fence systems did not function as exclosures. Duplicate reports on the same fence system were identified based on the size, region, and year of the fence installation, and only the latest information among the duplicates was retained in the final list. From each report on the final list, we extracted statements on the area enclosed by the fence (hereafter, fence size), the sum of the fenced areas within a system (size of the fence system), and the purpose of installation. The installation purpose was determined from statements in the introduction, results, and discussion sections of the literature. The purposes were then classified into seven categories, namely, vegetation cover restoration, plant species diversity restoration, conservation of specific plant species, soil protection, promotion of forest regeneration, agricultural area (including pasture) protection, and conservation of taxa other than plants. The final list comprised 174 fence systems from 25 countries, 21% (37 systems) of which were in Japan. Among the other countries, 54 fence systems were constructed in the USA, and

23 were constructed in Sweden. Using the final list, we compared quantiles of fence size and fence system size distributions to capture the characteristics of exclosures installed in Japan and other countries (Sect. 20.2.1). Additionally, we compared fence system sizes across study purposes in Japan and other countries to identify quantitative differences in the study focuses of different regions (Sect. 20.2.2).

20.2.1 Comparison of Deer-Proof Fence System Sizes in Japan and Other Countries

The mean fence system size in Japan (14,383 m^2) was smaller than that in the other 24 countries (154,764 m^2). Similarly, the median fence system size in Japan (800 m^2) was also smaller than in other countries (2304 m^2). Fence system size ranged from 238,100 m^2 to 5 m^2 in Japan and 6,850,000 m^2 to 10 m^2 in other countries. In Japan, one huge deer-proof fence system (9,800,000 m^2) was installed around Senjogahara, the largest bog in Japan. However, this system is not a true exclosure because deer can invade into the bog (i.e., inside fenced area) through roads where fences were not installed (Bansho and Amemiya 2010); thus, we excluded the system from our list.

A different picture was gained when fence systems sizes were compared using quantiles. In larger quantiles (i.e., quantiles larger than or equal to 60%, the fence system size was smaller in Japan than other countries (Fig. 20.1); whereas, in smaller quantiles (i.e., quantiles smaller than or equal to 40%), the fence system size was not significantly different between Japan and other countries (Fig. 20.1). Further, the mean and maximum fence sizes were far smaller in Japan than in other countries. Alternatively, the median fence size in Japan was larger than in other countries, due largely to the greater number of fences and smaller size of respective fences within a fence system in other countries; this trend was particularly evident when respective fence sizes were very small (i.e., 1 m^2). Moreover, only one fence system exceeded 100,000 m^2 (0.5%) in Japan, whereas 42 systems (2.7%) with equivalent or larger sizes were installed in other countries.

In conclusion, large exclosures are rarely installed in Japan compared with the global trend. Japan is characterized by steep and complex terrain, high precipitation, heavy snow, and frequent natural disasters compared with other countries (Takatsuki 2009; Cabinet Office Japan 2010), which may limit the number of large exclosures that can be installed and maintained.

20.2.2 Comparison of Deer-Proof Fence Purposes

To understand the characteristics of fence systems installed in Japan, we compared the number and size of fence systems for each purpose between Japan and other

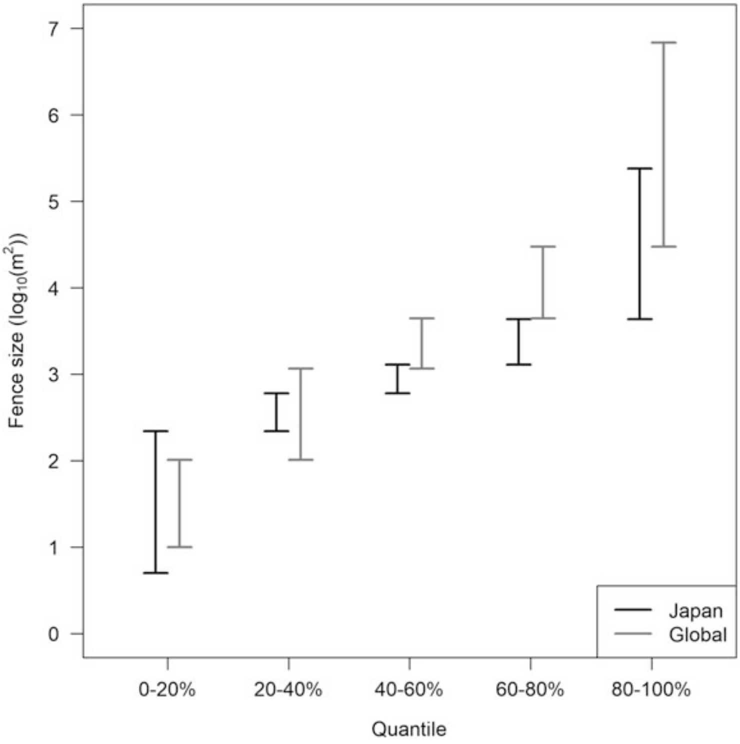

Fig. 20.1 Comparison of deer-proof fence system sizes (quantiles) in Japan and other countries. Bars show the size distributions in each 20% quantile

Table 20.1 Deer-proof fence sizes and conservation purposes in Japan and overseas

	Number of fence systems		Number of fences per system		Mean size of fence system (m^2)	
Purpose	Japan	Overseas	Japan	Overseas	Japan	Overseas
Vegetation cover	4	7	7.3	9.3	1405	220,991
Plant diversity	7	18	3.3	23.4	602	395,039
Specific species	6	10	9.2	12.9	7053	29,841
Soil	4	11	2.3	5.6	34,325	6678
Forest regeneration	7	66	4.3	9.0	659	128,897
Agriculture	6	8	2.8	23.1	10,874	203,271
Other species	3	17	19.7	6.8	90,950	119,991

countries (Table 20.1). Four notable features of the fence systems in Japan were identified. First, the size of fence systems installed to protect primary industrial fields (i.e., agriculture fields, pastures, and forests) was much smaller in Japan than in other countries. This difference could be attributed in part to the unit size of primary industrial fields—primary industrial fields comprise a much smaller facet of the land area in Japan compared with countries that have large and relatively flat land areas, such as the USA. It should be noted that there were few studies on fence systems to protect saplings planted for forest regeneration in Japan, although many fences were installed to protect planted saplings (mostly conifers) in Japan (Masaki et al. 2017). Second, the size of fence systems aimed to protect soil was about five times larger in Japan than in other countries. Soil erosion in steep forests is a serious problem caused by deer overgrazing in Japan; given that erosion often occurs at the scale of a mountain slope, large, watershed-scale fences are essential for prevention (Fukushima and Takeuchi 2008; Fukushima et al. 2013). Indeed, a 130,000 m^2 fence system in Ashiu forest research station, Kyoto, Japan, was installed to protect the area from soil erosion (Fukushima and Takeuchi 2008; Fukushima et al. 2013; Nakagawa 2019). The majority of studies in the soil protection category conducted outside Japan aimed to examine grazing-induced facilitation of the nutrient cycle or shortage of soil nutrients rather than to examine the effectiveness of fences for protecting soils from erosion. Third, the size of fence systems to enhance the recovery of vegetation cover and plant species diversity was smaller in Japan, whereas the largest fence system sizes were installed for these purposes in other countries. Unlike studies in other countries, the vast majority of Japanese studies on recovery of vegetation cover and plant species diversity compared the conditions of vegetation experimentally but did not investigate the change in community dynamics or community structures caused by deer grazing. Lastly, the size of fence systems for conserving particular plant species was much in Japan than in other countries.

20.2.3 Challenges to Better Utilize Deer-Proof Fence for Vegetation Conservation in Japan

Our systematic literature review highlighted that few large exclosures were installed in Japan. The natural conditions of Japan, such as steep and complex terrain and frequent natural disasters, may prevent the installation and maintenance of large exclosures. Furthermore, it is unrealistic to install numerous large exclosures to conserve entire ecological communities of concern or to protect soil erosion across Japanese terrestrial areas. To reduce the impact of overabundance of deer on vegetation or soil on a landscape scale, deer population management is preferred over deer-proof fences to conserve resources (i.e., time, budget, and human resources). However, it would be worth noting that complete exclusion of deer from a large area could alter or oversimplify vegetation because deer is a component of ecosystem, if deer is regarded as native to the area (Apollonio et al. 2017). Deer-proof fences are more effective than deer population management when vegetation protection is required on a small scale (e.g., patch scale).

Although Japan has a large proportion of forested area, the number of studies about fence systems installed to protect and enhance forest regeneration was limited, and the size of such systems was smaller compared with the global average. In

Japanese afforested regions, the regeneration of natural forests is necessary because the forestry industry is declining, which results in many planted forests left unmanaged (Sakai et al. 2006; Nagashima et al. 2009). At a landscape scale, deer population management would be preferred over fence installation in facilitating forest regeneration—plant species palatable to deer and intolerant to deer grazing, however, could be lost before decrease in deer population by the management. To ensure successful natural regeneration under deer pressure, more fence systems, which serve as refugia and source for landscape scale recovery (e.g., Iijima and Otsu 2018), should be installed and maintained in Japan. To facilitate the natural regeneration of Japanese forests, deer-proof fence installation should be, in some cases, accompanied by the removal of dwarf bamboo, which tends to dominate the understory and limit forest regeneration (Itô et al. 2014).

The size of Japanese fence systems to recover plant species diversity and conserve specific plant species was also much smaller than in other countries. Increasing the number and area of fence systems for these purposes would benefit vegetation conditions as well as improve our understanding of the effects of deer grazing on plant community dynamics. When a fence system is to be installed to conserve particular plant species, the size of the system must be large enough to protect the whole area needed by the species, which requires a preliminary survey of the distribution of conservation targets, the number and size of patches necessary for the species to inhabit, and connectivity among the patches.

20.3 Targets for Efficient Deer-Proof Fence Placement

To effectively retain ecosystem resilience and vegetation recovery capacity using deer-proof fences, it is essential to clarify an explicit aim for installing the fence system (e.g., maintain or restore plants), accounting for deer density, and the severity of deer grazing. Deer-proof fence installation is favored if the aim is to sustain species richness in ecosystems vulnerable to deer grazing (e.g., bog or alpine vegetation), facilitate vegetation recovery, and ensure the persistence of a population of spatial concern (e.g., rare or endangered species). However, even when the benefit of enclosing areas with the fences is evident, the total area that can be enclosed is generally limited by terrain conditions and/or management resources. Therefore, the prioritization of conservation targets (i.e., plant species to be protected by the fences or land units to install the fences) is essential to maximize management achievements. Likewise, the prioritization of areas to install fences is necessary when planning to transplant ground cover plants and trees to facilitate forest regeneration in a region with high deer density; in such regions, growth and reproduction of the planted species are largely restricted by severe grazing when fences are not concurrently installed. In this section, we provide targets for prioritizing conservation areas and actions along the deer grazing severity gradient.

20.3.1 Targets for Deer-Proof Fence Protection Where Deer Density Is Low

In regions with low deer density, protecting vegetation is generally easy to achieve when well-defined conservation targets are prioritized. When deer are at low density, their impacts on plants are not homogeneous across all plant species found in the region (Augustine and Frelich 1998; Itô et al. 2014). Deer graze on plant species selectively; thus, only plant species susceptible to deer grazing are impacted (Husheer et al. 2003; Bråthen et al. 2007). Plant species susceptible to grazing would be extirpated immediately if deer density increases (Husheer et al. 2003; Golodets et al. 2011). Further, plant species that are extirpated by intensive deer grazing may not re-emerge even after deer-proof fences are installed (Royo et al. 2010; Nuttle et al. 2014; Otsu et al. 2019), due to loss or reduction of the soil seed bank (Milberg 1995; Suzuki et al. 2013; Chap. 26). The number of regions harboring overabundant deer is predicted to rise rapidly in Japan due to land use changes (Takatsuki 2009; Saito et al. 2016), improved winter survival due to decreased snow accumulation (Loison et al. 1999; Saito et al. 2016), and declining numbers of predators and hunters (Potvin et al. 2003; Saito et al. 2016). Therefore, proactively conserving plant species, particularly species susceptible to grazing, before the predicted increase in deer density would increase the overall effectiveness of fence installation for retaining the regional species pool.

Plant species palatability, which can be approximated based on plant nutrition and chemical defense compounds, has been used as a criterion to estimate the susceptibility of plant species to grazing (Bråthen et al. 2007; Takatsuki 2009). Further, particularly in regions with low deer density, encounter tendency (tendency to be encountered by deer) should also be considered when estimating susceptibility to grazing. The degree of encounter tendency of a plant species is determined by both the distribution characteristics of the plant species and the frequency of deer visits to the site where the species inhabits (Shinoda and Akasaka 2017). Hence, the degree of encounter tendency depends on the environmental conditions that determine plant species distribution and areas frequently visited by deer (e.g., topology, distance from rivers, and canopy openness). In a simulation conducted by Shinoda and Akasaka (2017), the median number of species lost from a region in 20 years was approximately 1.8-fold smaller when exclosure areas were selected based on both palatability and encounter tendency than when the areas were selected based on palatability alone. Therefore, concurrent consideration of plant palatability and encounter tendency could improve the performance of conservation target prioritizing for establishing exclosures to safeguard regional plant species diversity, particularly when deer density in the region is low.

20.3.2 Targets for Deer-Proof Fence Protection Where Deer Density Is High

When aboveground vegetation is largely reduced by grazing, plant species distribution is not a feasible criterion for prioritization. At this stage, protecting the source of the resilience of focal plant communities becomes the primary goal to retain the capacity of plant species to recover after suppressing deer density. Therefore, areas with expected decreases in seed bank density would be prime targets at this stage. However, the degree of decrease in the source of resilience (i.e., seed bank density) due to deer grazing is not spatially uniform (DiTommaso et al. 2014; Tamura 2016; Shinoda and Akasaka 2020). For example, the reduction of seed bank density caused by deer grazing is more pronounced with increasing canopy openness. In a case on an island in Hokkaido, Northern Japan, the degree of grazing impacts on seed banks within plots located outside exclosures was approximately one-tenth of that in plots within exclosures when canopy openness was 65%, although the degrees were almost identical in closed-canopy plots (Shinoda and Akasaka 2020). Given that canopy gaps often facilitate germination, deer tend to graze seedlings in these areas, decreasing the number of seeds reserved in the soil bank. In addition, the occurrence probability of a particular plant species in the seed bank also decreased significantly with increasing slope steepness (Shinoda and Akasaka 2020). Therefore, identifying areas for fence installation where seed bank density is prone to decrease is crucial for maintaining the resilience of plant communities in regions with high deer density and limited management resources. In particular, understory and seedling regeneration is facilitated under open canopy areas if deer grazing does not occur (Mladenoff 1990; Bazzaz 1996). Therefore, areas with recently opened canopy gaps would be candidates to target for establishing exclosures to ensure the recovery of plant species.

Compared with aboveground changes, early detection of decreases in seed bank density and soil degradation is difficult. Severe and long-term deer grazing could reduce seed banks before any decrease in aboveground vegetation is apparent (Tamura 2016; Shinoda and Akasaka 2019; Chap. 26). Moreover, long-term grazing degrades soil conditions, which could inhibit the growth and establishment of seedlings (Suzuki and Ito 2014; Harada et al. 2020). Installing fences is important not only for conserving plant communities but also for the detection of decreases in seed bank density and soil degradation, even when the effects of deer grazing on plant communities do not appear to be severe.

20.3.3 Restoring Vegetation with Deer-Proof Fences After Vegetation Collapse

Vegetation seriously damaged by intense and frequent deer grazing cannot function as it does in its pristine state. For example, heavily damaged vegetation cannot produce litter, maintain soil humidity, or prevent soil runoff (Gass and Binkley 2011; Cournane et al. 2011). To retrieve these functions, management efforts such as introducing ground cover plants, seeds, and saplings have been conducted, often using pioneer plant species (Gómez-Aparicio et al. 2004). Pioneer plant species are characterized by rapid growth in open habitats, making them suitable for regeneration efforts. However, such species are also susceptible to deer grazing because they possess few chemical defenses (Dalling et al. 2009; Nagashima et al. 2019). Therefore, deer-proof fences must be installed concurrently with restoration actions to ensure positive management outcomes.

In Japan, vegetation functions are often restored to prevent soil runoff on steep slopes. However, the installation and maintenance of fences on steep slopes pose several difficulties. Fences on steep slopes are more prone to be damaged by materials sliding down the slopes, such as debris, eroded soils, fallen trees, and snow. Even a small corruption of the fence could allow deer to invade the exclosure and graze recovering vegetation. Additionally, taller fences are required on slopes because deer can easily jump inside low exclosures from the upper slope. Although fences are generally installed perpendicular to the ground surface to create an enclosed area free from grazing, grazing-free spaces could also be created by placing fences horizontally 20 cm from the ground surface (Fukui et al. 2013).

20.4 Conclusion

Deer-proof fences are an effective tool to protect and temporally restore plant communities in a small scale, although fence installation does not fundamentally solve all problems caused by deer. When installing large deer exclosures is not feasible, prudent consideration of the fence system size and conservation targets is essential, as these areas can serve as refugia or seed sources for the region. Even when deer density in a region is low, deer populations can grow dramatically in a short time. Therefore, even after the initiation of deer population management, plant species or seed banks could disappear from the region before the management goal is achieved. To maximally ensure the persistence of plant species and seed banks in a target region, proactive installation of fences is a useful strategy that is applicable to many regions.

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Chapter 21
Vertebrate Scavenging on Sika Deer Carcasses and Its Effects on Ecological Processes

Akino Inagaki, Maximilian L. Allen, Tomoko Naganuma, and Shinsuke Koike

Abstract The impacts of sika deer on ecological communities often focus on the effects of "alive" deer, but how "dead" deer affect organisms and the environment currently receives little attention. Dead animals (i.e., carcasses) are a high-quality food resource for scavengers that provide ecosystem services, and scavenging plays an important role in ecosystem stability. Forest ecosystems in Japan have an overabundance of deer and need constant population control via culling. Consequently, the deer carcasses from natural mortality and hunting and/or culling by human are a large food resource for many vertebrate scavengers. In the forest ecosystem of Honshu Island, we documented a vertebrate scavenger guild that feeds on deer carcass, which is composed of six mammals and three birds. Vertebrate scavenging is widespread, and the scavenging links from carcass to vertebrate scavengers are one of the essential energy transfers in food webs. Furthermore, sika deer carcasses were consumed entirely in about 1 week; thus, vertebrate scavengers contribute ecosystem services to remove potentially infectious carcasses from ecosystems. Future carcass availability related to overabundant deer populations and their management could alter the function of the scavenging community. Considering carrion management is a critical aspect in evaluating the widespread impact of deer and their ecological processes and could lead to proper ecosystem management.

A. Inagaki (✉)
United Graduate School of Agricultural Science, Tokyo University of Agriculture and Technology, Fuchu, Japan
e-mail: akino.inagaki@gmail.com

M. L. Allen
Illinois Natural History Survey, University of Illinois, Champaign, IL, USA
e-mail: maxallen@illinois.edu

T. Naganuma · S. Koike
Institute of Global Innovation Research, Tokyo University of Agriculture and Technology, Fuchu, Japan
e-mail: tama.827dx@gmail.com; koikes@cc.tuat.ac.jp

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21.1 Introduction

The direct impacts of sika deer (*Cervus nippon*) on ecosystems often focus on the negative processes of deer foraging and trampling behavior. For example, the increased browsing and debarking pressure associated with overabundant deer populations cause serious damage to plant survival biodiversity and structure (Akashi and Nakashizuka 1999; Takahashi and Kaji 2001; Suda et al. 2001; Yokoyama et al. 2001; Nomiya et al. 2003; Suzuki et al. 2008; Takatsuki 2009; Nagaike 2012). In addition, the trampling by high densities of sika deer leads to physical disturbance and loss of the soil surface (Tsujino and Yumoto 2004; Niwa 2020). These impacts caused by “alive” deer have been well-studied (see Chaps. 16 and 23), but how “dead” deer affect organisms and their environment has received very little attention.

Dead animals (i.e., carcasses) are a high-quality and ephemeral food resource for scavengers that consume it and provide ecosystem stability and services. Scavenging is a widespread feeding behavior (Wilson and Wolkovich 2011; Beasley et al. 2019), and various biological groups from decomposers (e.g., invertebrates and microbes) to vertebrates shape the characteristic scavenging communities (DeVault et al. 2003). Vertebrate scavenging from carcasses shapes energy transfer links in food webs, and these additional links promote food web complexity and stability (Selva and Fortuna 2007; Wilson and Wolkovich 2011). Vertebrate scavengers also remove carcasses that are a source of harmful pathogens from ecosystems quickly by consuming carrion (DeVault et al. 2003; Moleón et al. 2014; Inger et al. 2016). In cases of carrion with large biomass, like ungulate carcass, a greater number and more diverse scavenger species are attracted to compete for the nutrition from the carcass, contributing to biodiversity maintenance (Barton et al. 2013; Moleón et al. 2015).

Japanese forests have high-density sika deer populations, and ongoing population management is being implemented by government. For example, approximately 465,700 deer were culled throughout the year by population management and approximately 137,200 were hunted in the recreational hunting season (generally 15 November to 15 February) in 2019 (Ministry of Environment, Japan 2020). These deer carcasses from hunting, culling, and natural mortalities may be an important food resource for vertebrate scavengers. However, deer carcass as a food resource has been overlooked, thereby lacking common, widespread obligate scavenger (i.e., that feed solely on carrion) species, like vultures, or large predators that regularly kill ungulates (see study area for a description of scavenger community) in Japan. Furthermore, it is difficult to find and observe natural mortalities because mountain forests often consist of steep terrain. For these reasons, little is known about the fate of these deer carcasses and the vertebrate scavenging process of deer carcass in Japan.

In this chapter, we report the utilization and consumption time of deer carcasses by vertebrate scavengers. We also discuss the ecological role of vertebrate scavengers and how changes in the deer population (i.e., the availability of deer carcass) may alter scavenging and its ecological function.

21.2 Material and Methods

21.2.1 Study Area

Nikko National Park is located in central Honshu Island (mainland Japan) at latitude 36°36′N–37°05′N, longitude 139°19′E–139°51′E. The area occupies 1159 km^2 and at elevations between 300 and 1300 m. The climate is temperate, with the mean annual temperature of 7.7°C and the mean annual rainfall of 2131 mm. The forest is characterized by deciduous broadleaved forests (composed mainly of *Quercus serrata*, *Q. crispula Blume*, and *Cerasus jamasakura*), conifer plantation forests (comprising mainly *Cryptomeria japonica*, *Chamaecyparis obtusa*, and *Larix kaempferi*), and also patchy mixed forests. The bamboo grasses (*Sasa* spp.) primarily covered each type of forest floor.

Sika deer are the largest herbivorous mammal in the forest, and the estimated population of sika deer in the study area is 13,429 deer (11.59 deer/km^2) in 2019 (Oze-Nikko National Park Wide-Area Council for the Control of Sika Deer 2020). Wolves (*Canis lupus*) were extirpated by 1905 (Hiraiwa 1981), and none of the other predators kill adult deer, although Asian black bears (*Ursus thibetanus*) are known to kill neonatal deer (Hashimoto and Takatsuki 1997). The mammalian scavengers on deer carcasses include Asian black bear, wild boar (*Sus scrofa*), red fox (*Vulpes vulpes*), raccoon dog (*Nyctereutes procyonoides*), masked palm civet (*Paguma larvata*), and Japanese marten (*Martes melampus*) (Inagaki et al. 2020; Fig. 21.1a). The bird scavengers include jungle crow (*Corvus macrorhynchos*), black kite (*Milvus migrans*), and mountain hawk-eagle (*Nisaetus nipalensis*) (Inagaki et al. 2020, Fig. 21.1b).

21.2.2 Monitoring of Deer Carcass

We used video camera traps to observe the vertebrate scavenging of deer carcasses. From June to November in 2016 and 2017, we placed 42 fresh deer carcasses (18 male and 24 female; mean weight = 43 kg [range 10–70 kg]) that had not been scavenged in the mature deciduous broadleaved forests and patchy mixed forests (Inagaki et al. 2020). We secured the deer carcasses to the nearest tree using wire rope to prevent them from being removed by scavengers. We programmed the camera (Ltl-Acorn 6210 MC; Green Bay, Wisconsin, USA) to record 30-s videos at each trigger with a 30-s refractory period. We monitored a carcass until there was little available carrion (e.g., bones and skin) for vertebrate scavengers remaining.

Fig. 21.1 Vertebrate scavenger species (**a**, mammal; **b**, bird) on deer carcass on Honshu Island, Japan. (**a**) The species starting from the upper left, Asian black bear, wild boar, and raccoon dog, and from the lower left, red fox, Japanese marten, and masked palm civet. (**b**) The species starting from the left, mountain hawk-eagle, black kite, and jungle crow

21.2.3 Utilization of Deer Carcass

To evaluate the utilization of deer carcass by vertebrate scavengers, we determined (1) scavenging frequency, (2) feeding duration, and (3) seasonal differences of scavenging frequency among species and groups (i.e., mammal vs. bird).

Scavenging Frequency We calculated the number of deer carcasses that each species scavenged (fed on carrion). We used Fisher's exact tests to determine differences in the proportions of scavenged carcasses between mammals and birds. We then tested pairwise comparisons with Fisher's exact tests using Holm's multiple comparison adjustment in RVAideMemoire package (Hervē 2019) to determining differences in the proportions of scavenged carcasses among scavenger species.

Feeding Duration We calculated total feeding times (minutes) at each deer carcass for each species. In cases where there were more than five jungle crows in one video, we estimated total feeding time by summing the feeding time of five randomly selected individuals and multiplying this value by the maximum number of individuals during the visit divided by five. We used Wilcoxon rank sum test to examine differences in the mean feeding times between the groups (mammals vs. birds).

Seasonal Differences of Scavenging Frequency We classified the seasons as summer (June to August) and autumn (September to November). We tested for differences in the proportions of scavenged carcasses seasonally between groups (mammals vs. birds) and among species using Fisher's exact test. We then used Wilcoxon rank sum test to examine differences in feeding duration seasonally between groups (mammals vs. birds).

21.2.4 The Elapsed Time of Deer Carcass Consumption

To determine the elapsed time of deer carcass consumption, we calculated the period from when we set out each carcass until all edible portions except bones and skins were consumed (Sebastián-González et al. 2020).

21.3 Results

21.3.1 Utilization of Deer Carcass

We monitored 42 deer carcasses (summer = 20 deer, autumn = 22 deer), and all the carcasses were scavenged by at least one scavenger. We documented scavenging by mammals (97.6%; $n = 41$) at a significantly higher number of carcasses than birds (42.9%; $n = 18$) ($p < 0.001$, Fig. 21.2). The most frequent scavenger species were raccoon dogs (85.7%; $n = 36$) and secondly, Asian black bears (73.8%; $n = 31$, Fig. 21.3). They scavenged at a significantly higher number of carcasses than other scavengers ($p < 0.001$). In contrast, the least frequent scavengers were masked palm civets (2.4%; $n = 1$), black kites (9.5%; $n = 4$), and mountain hawk-eagles (11.9%; $n = 5$, Fig. 21.3). Scavenging by these species was at a significantly lower number of carcasses than other scavengers ($p < 0.001$).

For feeding duration, the mean feeding time (min) at carcasses was longer for mammals (80.2 ± 90.0 SD min) than for birds (29.3 ± 80.0 min, $p < 0.001$). Among

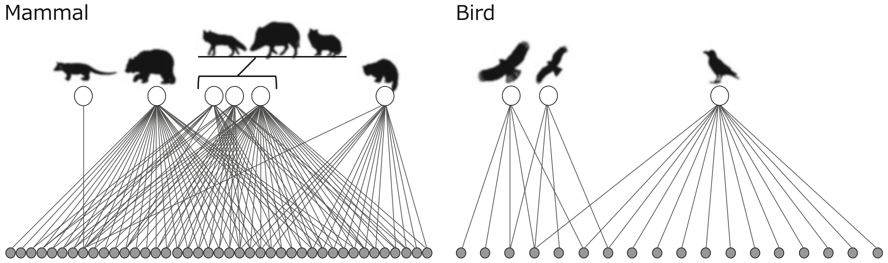

Fig. 21.2 Bipartite graphs depicting scavenging interactions between the vertebrate scavengers (open circles) and deer carcasses (filled circles)

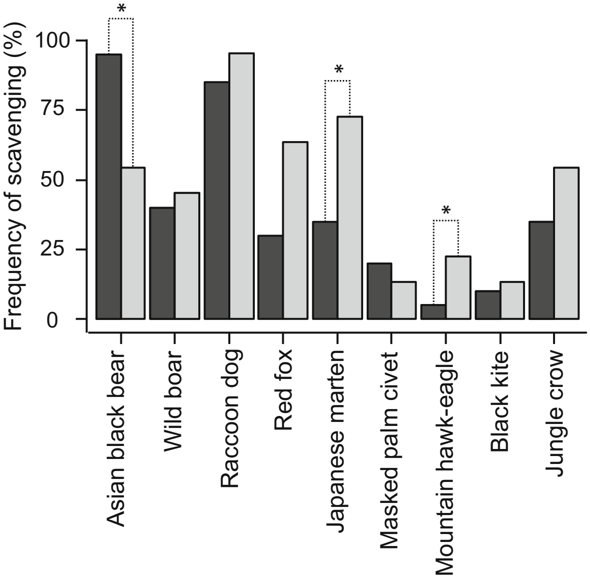

Fig. 21.3 The frequency (%) of scavenging for each species. Dark colors indicate summer; light colors indicate autumn. The asterisks indicate significant differences between summer and autumn ($p < 0.05$)

scavenger species, Asian black bears (36.9 ± 34.9 min) and raccoon dogs (52.6 ± 78.1 min) fed for longer durations (Fig. 21.4).

For seasonal differences of scavenging frequency, mammals had significantly higher scavenging frequency ($\text{frequency}_{\text{summer}} = 100\%$, $p_{\text{summer}} < 0.001$; $\text{frequency}_{\text{autumn}} = 95.5\%$, $p_{\text{autumn}} < 0.001$) and mean feeding time ($\text{mean}_{\text{summer}} = 53.1 \pm 53.4$ min, $p_{\text{summer}} = 0.023$; $\text{mean}_{\text{autumn}} = 106.0 \pm 108.3$ min, $p_{\text{autumn}} < 0.001$) than birds ($\text{frequency}_{\text{summer}} = 40.0\%$, $\text{frequency}_{\text{autumn}} = 45.5\%$; $\text{mean}_{\text{summer}} = 13.1 \pm 20.4$ min, $\text{mean}_{\text{autumn}} = 37.5 \pm 95.8$ min) in both seasons. The scavenging by Asian black bears decreased significantly from summer to autumn ($p = 0.0042$), while scavenging by Japanese martens and mountain hawk-eagles significantly increased ($p_{\text{Japanese martens}} = 0.0289$, $p_{\text{mountain hawk-eagles}} = 0.0492$, Fig. 21.3). Red foxes also slightly increased the scavenging frequency from summer to autumn ($p = 0.0577$, Fig. 21.3).

21.3.2 The Elapsed Time of Carcass Consumption

The mean carcasses consumption time was 6.8 days (median = 6.5 days) with ranges from 2.3 to 16.5 days. We illustrate the process of carcass decomposition for one carcass that was consumed at 6.5 days in Fig. 21.5. This carcass was detected first by raccoon dog at about 3.6 days after carcass placing and then scavenged by Asian black bear, raccoon dog, and red fox. We also observed invertebrate colonization mainly composed of flies and maggots.

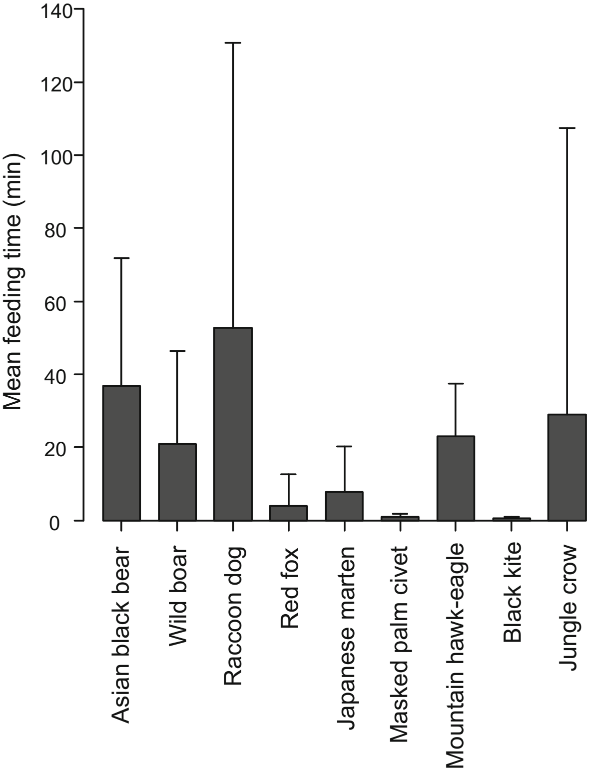

Fig. 21.4 The mean feeding time (min) for each species. The vertical solid bars indicate standard deviations (SD)

Fig. 21.5 An example of the consumption process of a deer carcass across 6.5 days. This deer carcass was placed on October 6, 2016 (the picture to the left), and totally consumed by October 13

21.4 Discussion

21.4.1 Vertebrate Scavenging and Its Ecological Role

Forest ecosystem in Honshu includes a vertebrate scavenger guild at deer carcass that is composed mainly of omnivorous carnivores, as well as a few forest bird species (Inagaki et al. 2020). All deer carcasses that we placed were scavenged by at least one vertebrate species, but scavenging by birds was likely restricted by the dense tree canopy and grass understory (Ogada et al. 2012). Raccoon dogs and Asian black bears are key scavengers in this system, because they fed on more deer carcasses and for longer durations than other scavengers. Despite little previous study, we found that scavenging is widespread as in other regions (e.g., Mateo-Tomás et al. 2015; Sebastián-González et al. 2020), and "dead" deer carcasses are a high-quality food and pulsed resource for vertebrate scavengers. Thus, scavenging links from carcasses to vertebrate scavengers provide one of the important energy transfers in food webs (Selva and Fortuna 2007; Wilson and Wolkovich 2011; Moleón et al. 2014).

Considering the direct interactions between deer carcass and vertebrate scavengers, how dependent each scavenger is for carrion should not be overlooked for their individual health and population maintenance. For example, the high utilization of carcasses by raccoon dogs overall suggest that they may be heavily dependent on nutrition from carrion. In other words, variation in the carcass availability may have an effect on the diet of raccoon dogs. Some scavenger species like Asian black bear and mountain hawk-eagle changed their frequency of carcass utilization by season. Omnivores are known to switch their feeding strategies by season in accordance with the availability of their primary food sources (Inagaki et al. 2020). In addition, carrion is an important supplemental food resource in severe winters (Tannerfeldt et al. 1994). Therefore, not only carcass availability but also other food sources and their phenology may affect scavenging. Quantifying how each scavenger depends on carcasses and the relevance with other food resources under various food conditions could lead to understanding the dynamics of facultative scavenging on food webs in the future.

Another important aspect of scavenger ecology is their ecosystem services, as shown by sika deer carcasses being consumed in about 1 week on average. Mean consumption time in temperate habitats has been reported to be 11.3 days in black-tailed deer (*Odocoileus hemionus columbianus*; Allen et al. 2014), 10.0 days in wild boar (Turner et al. 2017), and 3.1–4.2 days in ungulates (Mateo-Tomás et al. 2015; Morales-Reyes et al. 2019), where obligate scavengers are present. Also, it is 8.8 days in roe deer (*Capreolus capreolus*), where obligate scavenger is absent (Krofel 2011). As these results show, sika deer carcasses in Japan were consumed at a relatively faster rate, despite there being no predators of adult deer or obligate scavengers in the ecosystem. Considering the widespread scavenging by vertebrates, vertebrate scavengers do contribute to the removal of carcass from ecosystems. In general, large predators or vultures are key species that promote carcass consumption through interspecific interactions (Selva and Fortuna 2007; Mateo-Tomás et al. 2015). On the other hand, invertebrates that are common in certain environments also can compete with vertebrates and accelerate the decomposition process (Beasley et al. 2012; Pereira et al. 2014). To understand the ecological role of vertebrate scavengers, it is necessary to examine what contributes to the consumption of deer carcasses from both biological factors (e.g., carcass size, interaction between vertebrates and invertebrates) and non-biological factors (e.g., environmental characteristics) and how ecological significance vertebrate scavengers has to faster removal of carcasses from ecosystem.

21.4.2 Deer Impact on Scavenging Community

The availability of deer carcasses related to deer overabundance and its population management (i.e., anthropogenic carrion) could alter scavenging function, consequently triggering changes to ecological processes at various scales. Oro et al. (2013) suggested that aspects of biological fitness at an individual level (including body mass, fecundity, survival, and dispersal) are directly affected by the biomass of anthropogenic carrion. These effects on individuals also lead to effects at the population level such as population size and fluctuations, foraging behavior, and diet. In addition, the ecosystem and populations could be changed not only relation to interspecific competition and food webs but also species composition, habitat characteristics, and human-wildlife conflict. Indeed, the diet of Asian black bear has changed to high deer dependence with habitat conditions caused by overabundant sika deer (Koike et al. 2013). Thus, carrion availability is the foundation of scavenging dynamics and its interspecific interactions.

If natural and anthropogenic carcasses increase with their increasingly overabundant population and switch from competitive to excessive food resource, the impact of scavenging on ecological processes will require special attention. In Japan, there has not been a management method based on scientific knowledge established for the treatment of deer carcasses resulting from intense population control for overpopulated deer. According to “Wildlife Protection and Hunting Management Law,” captured animals should be taken out in principle, only in unavoidable cases should they be buried in an appropriate manner that does not affect the ecosystem. However, in reality, the waste in forest is often buried or remains on site (Yamada 2018). In this gap between the current system and the situation, it is not clear how impact the carcass has on the ecosystem. It needs for further research to accumulate scientific knowledges in carcass management, such as whether carcasses should be left behind or removed. Simultaneously, fundamental knowledge that reveals relationships between deer carcasses and its scavengers and their ecological function should be further investigated, not only for vertebrates but also for invertebrates. In summary, considering carrion management is important to evaluate widespread impacts of deer and their ecological process and is needed for proper ecosystem management.

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Chapter 22

Impacts of Sika Deer Overabundance on the Structure and Functions of Dung Beetle Communities in Forest Ecosystems

Shinsuke Koike, Kahoko Tochigi, and Masashi Soga

Abstract Deer overabundance changes the vegetation structure and affects various ecosystem members, particularly the insects, through cascade effects. Among insects, dung beetles are affected by the increase in deer population in various ways. For example, the increase in dung consumption as a food resource has a positive impact, while the decrease in vegetation has a negative impact due to the decrease in food availability by aridification feces. In addition, the effects of increased deer population are different for adults and larvae; its effects are particularly significant for large-bodied dung beetles because of the influence of the mammalian fauna on the resource usability of larvae. In addition, dung beetles have various functions in several ecosystems, including fecal decomposition and seed dispersal. Therefore, the increase in deer population may affect the entire ecosystem through changes in the ecosystem functions of dung beetles. Understanding how the increase in large herbivore populations affects ecosystem functions is important to evaluate the ecological consequences of their overabundance and ultimately manage their populations appropriately.

S. Koike (✉)
Institute of Global Innovation Research, Tokyo University of Agriculture and Technology, Fuchu, Japan
e-mail: koikes@cc.tuat.ac.jp

K. Tochigi
United Graduate School of Agricultural Science, Tokyo University of Agriculture and Technology, Fuchu, Japan
e-mail: k.koro722@gmail.com

M. Soga
Graduate School of Agricultural and Life Sciences, The University of Tokyo, Bunkyo-Ku, Japan
e-mail: asoga@mail.ecc.u-tokyo.ac.jp

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22.1 Introduction

The dramatic increase in the populations of large mammalian herbivores (hereafter, large herbivore overabundance) has become a major ecological issue, particularly in the northern hemisphere (Côté et al. 2004), affecting the structure, dynamics, and processes of forest ecosystems. For example, large herbivores alter the vegetation structure and composition through browsing (Tanentzap et al. 2012) and bark stripping (Iijima and Nagaike 2017), with the former inducing the loss of vegetation cover and the dominance of non-palatable plant species, and the latter leading to dieback of overstory trees (Nagaike 2019).

In addition, trampling by large herbivores affects soil properties, such as hardness and saturation capacity (Kumbasli et al. 2010). Large herbivore overabundance can affect other animal species (e.g., insects and birds) by reducing the availability of food resources and changing the condition of their habitat—the so-called cascade effect (Allombert et al. 2005; Teichman et al. 2013). To manage and conserve the ecosystems and ultimately reverse the ecological consequence of large herbivore overabundance, it is first necessary to understand and predict how biological communities respond to large herbivore overabundance (Côté et al. 2004).

To investigate the relationships between species life history traits and their sensitivities, insects are excellent model organisms. This is because many insect species have species-specific life history traits, and they respond quickly to environmental changes (Maleque et al. 2009; Sumways 2007). Indeed, previous studies have shown that insects are one of the most likely taxa to be affected by large herbivore population changes (Iida et al. 2016a; Melis et al. 2007; Stewart 2001; Teichman et al. 2013).

Additionally, large herbivore overabundance can change the structure and composition of biological communities and alter the ecosystem functions that they provide. Insects have a wide range of ecosystem functions in forests that are crucial to maintaining ecosystem stability, including pollination, seed dispersal, nutrient cycling, and carcass decomposition (Brew et al. 1989; Kevan and Baker 1983; Koike et al. 2012; Sugiura et al. 2013). Indeed, it is generally accepted that the alteration of biological communities, such as the decrease in functional diversity and change in species composition, is closely linked to the ecosystem's functional ability (Elmqvist et al. 2003; Larsen and Forsyth 2005; Naeem and Wright 2003; Snelgrove et al. 2014; Sugiura et al. 2013).

Among various insects, dung beetles are insects with strong ties to large mammalian herbivores and ecological functions. Dung beetles have generalist diets; therefore, resource shifts are easy. They shift resource depending on the changes in the population density of individual animal species. With these changes, dung beetles may select higher-quality feces (higher nitrogen, amino acid, and fatty acid contents) or more abundant feces (Hanski et al. 2008; Stavert et al. 2014). In contrast, until they metamorphose, larval dung beetles eat the feces in which they were laid as eggs, i.e., belonging to a single animal species. Additionally, the larval digestive system differs from that of adults. Unlike adults, larvae can feed on feces containing plant fragments. Therefore, larvae can feed on a wider range of animal feces, and the amplitude of larval resource niche may be greater than that of adults at the species level (Bourg et al. 2016). Thus, the changes in fauna or faunal population density or food resource may readily affect the larval diet more than the adult diet.

Additionally, the decomposition of mammal dung is a key process in forest ecosystems that is largely performed by insects (Didham et al. 1996). Dung beetles are one of the main taxa involved in dung decomposition (Nichols et al. 2008), with both the larvae and adult dung beetles consuming the dung of other animals. Dung beetles break down fecal matter oftentimes by burying it, which contributes to the transport of essential nutrients into the soil (Bertone et al. 2006) and soil mixing (bioturbation) (Brown et al. 2010; Nichols et al. 2008). Dung beetles can also act as secondary seed dispersers as they bury some of the seeds that are present in dung in the soil, reducing the probability of seed predation by rodents and preventing drying (Koike et al. 2012).

Therefore, this chapter provides an overview of the effects of the increase in deer population on dung beetle communities, larval resource utilization, and fecal decomposition functions.

22.2 Effect on the Dung Beetle Community

Large herbivore overabundance can have both positive and negative effects on dung beetle communities, as large herbivores provide food resources (i.e., dung) to dung beetles and change the vegetation and soil properties through browsing, which is likely to degrade the habitat conditions for dung beetles (Barbero et al. 1999; Davis et al. 2014). It is known that the magnitude and direction of dung beetle responses to the increasing abundance of large herbivores depend not only on the magnitude of the increase (see Kanda et al. 2005) but also on the life history and ecological traits of the dung beetles, such as their feeding behavior and body size (Koike et al. 2014). Here we would like to introduce the case study on Lake Toya (Iida et al. 2016b).

Lake Toya, located in western Hokkaido, northern Japan, provides an ideal study site to investigate the long-term impacts of deer overabundance on ecosystems. On Nakanoshima Island (476.7 ha, hereafter, island), which is one of the islands situated within Lake Toya, the sika deer (*Cervus nippon* Temminck (Cervidae)) density was over 50 deer/km^2 (Ikeda et al. 2013). In contrast, in the areas around Lake Toya (hereafter, lakeshore), and at the time of the current study, the deer density was approximately 1.1×10^{-2} deer/km^2 (Akaba et al. 2014), which is considerably lower than the density in the island. Thus, there are significant differences in the vegetation structure among the sites.

We established 30 sampling plots which were 100 m apart from each other (along the 3-km sampling transect) in each of the island and lakeshore sites. In both sites, we sampled dung beetles using pitfall traps baited with cattle dung. The pitfall traps were constructed using plastic containers (22.5 cm in diameter and 26.6-cm deep) and plastic cups (8.3 cm in diameter and 11.5-cm deep). Then, the plastic cups

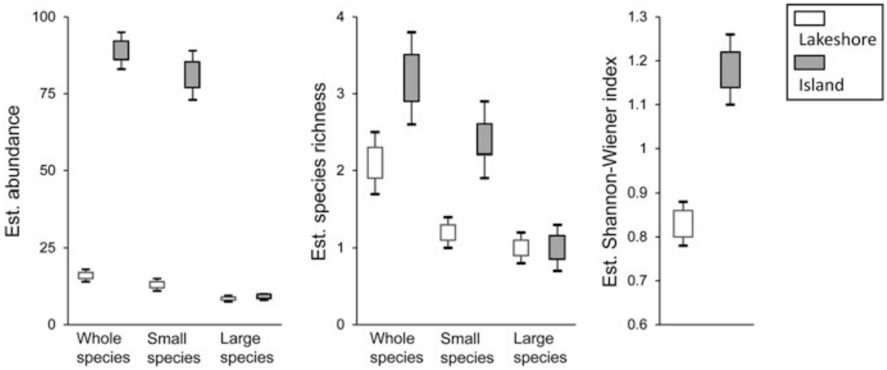

Fig. 22.1 (left) Abundance of each body size per plot in island and lakeshore sites estimated by generalized linear models (GLMs) (see Iida et al. 2016b for more details about the statistical analysis). (center) Species richness of each body size per plot in island and lakeshore sites estimated by GLMs. (right) Shannon–Wiener index of dung beetles per plot in island and lakeshore sites estimated by GLMs. The body sizes were classified into small and large species. Asterisks indicate a significant difference ($p < 0.05$)

containing the cattle dung were hung inside the container using wires. The plastic roofs were set on the traps to prevent interference from rain and fallen leaves. One trap was set per plot. The surveys were conducted during early September 2012 and 2013. Additionally, the dung beetle species collected in the field were divided into different size groups according to body length (see Koike et al. 2014). The dung beetles were divided into groups for small or large species (small, <10 mm; large, ≥10 mm).

In a series of surveys, a total 2902 dung beetles (five species, large type, *Copris ochus*, *Geotrupes laevistriatus*; small type, *Caccobius jessoensis*, *Onthophagus ater*, *Liatongus phanaeoides*) were collected. All species were tunneler type. The comparisons between species richness, abundance, and diversity index of species between the island and lakeshore sites were summarized in Fig. 22.1. The abundance (GLMs: $p < 0.001$) and species richness (GLMs: $p = 0.008$) of all species in the island site were higher than in the lakeshore site (Fig. 22.1a). Although the abundance and species richness of small species were similarly higher in the island site than in the lakeshore site (GLMs: $p < 0.001$; Fig. 22.1b), those were not the case for large species (abundance: $p = 0.78$, species: $p = 0.90$). The mean species diversity index was higher in the island site than in the lakeshore site (GLMs: $p < 0.001$; Fig. 22.1c).

This study demonstrated that the increase in the sika deer population in Lake Toya significantly changed both the abundance and species richness of beetle species. Dung beetles responded positively to deer overabundance, with abundance, species richness, and diversity index higher in the island site. Adult and larvae dung beetles utilize the feces of mammals as their main food resource (Andresen and Laurance 2007; Nichols et al. 2009). Hence, the deer overabundance in the island site is likely to produce a greater quantity of feces as a food source for dung beetles as compared to the lakeshore site. Indeed, Kanda et al. (2005) reported a positive relationship between dung beetle abundance and deer density.

Although the abundance of small dung beetle species was significantly higher in the island site than in the lakeshore site, of the abundance of large species did not differ between the two sites. This result suggests that small species are likely to favor a deer-abundant environment. In contrast to our results, in Honshu island, Japan, Koike et al. (2014) observed that small species did not prefer environments with higher deer density. One possible reason for the difference would be the difference in dung usage among the study species. Koike et al. (2014) found that small species tended to be dwellers, which simply lay their eggs into the dung on the ground (Camberfort and Hanski 1991), causing drying because of sunlight exposure. This results from deer overbrowsing, negatively affecting these species. Conversely, in this study, the majority of small species were tunnelers, which are species that bury dung under the ground before oviposition (Camberfort and Hanski 1991). Because of dung burying, the tunnelers are not influenced by the drying on the ground surface.

This study provides a piece of evidence that the increase in deer population alters the species richness, abundance, and diversity of dung beetles. However, the relationship between the dung beetle fauna and deer density should be treated with caution, as there are cases where no clear trend is found, as in the present study, or where only large-sized species are known to vary in number.

22.3 Potential Impact on Larval Resource Utilization

The dung beetle food resources increase with the increase in sika deer population, affecting their community. Additionally, the overabundance of sika deer affects other sympatric mammals. The understory reduction by the deer, dung decomposition, or both increases raccoon dog (*Nyctereutes procyonoides*) and badger (*Meles anakuma*) population densities by increasing earthworm abundance, their main food resource. Conversely, rodents have declined in the understory, negatively affecting the predators, such as red foxes (*Vulpes vulpes*) and Japanese martens (*Martes melampus*) (Seki et al. 2014). The diets of Asian black bears (*Ursus thibetanus*) and brown bears have also changed, as they eat more deer meat (Koike et al. 2013a, b; Sato et al. 2004). Thus, the overabundance of sika deer may affect the relative amounts and compositions of feces excreted by each mammal species. Therefore, the diet of dung beetles may change because of the changes in the density of sika deer populations.

We introduce the case study on the relationship between the increase in sika deer population density and the diet of dung beetle larvae (Yama et al. 2019). To evaluate the dietary changes of larval dung beetles, we focused on the adult exoskeleton. Generally, insects that completely metamorphose form an exoskeleton; its molecular composition varies depending on the food ingested by the larvae (Stavert et al. 2014). Furthermore, we estimated the larval diets of dung beetles by analyzing the nitrogen stable isotope ratios in adult dung beetles' exoskeletons. Stable nitrogen isotope ratios exhibit stepwise enrichment through the food chain, with increasing values of δ^{15}N (DeNiro and Epstein 1981). Therefore, the values between the herbivores and carnivores should differ notably (McFadden et al. 2006). This study collected different dung beetle species in two study areas where sika deer population densities differed; then, we analyzed the nitrogen stable isotope ratios in the exoskeletons of the beetles and compared the values between the areas with different sika deer population densities to clarify the difference in the larval diets of dung beetles.

The study was conducted in the Ashio–Nikko mountain area of central Japan (36.54–36.80°N, 139.22–139.49°E). We established 20 study sites, all in forested areas comprising deciduous trees. The study sites were split according to deer density: high (>15 deer/km^2) (HD) and low (<5 deer/km^2) (LD); 10 study sites were set up in each of the different sites of deer density. The relative abundance index (total number of individuals photographed/(number of cameras × number of days as a unit to compare the relative frequencies of images) of the following mammals were calculated: sika deer (LD: 0.26; HD: 0.57), badgers (LD: 0.03; HD: 0.02), raccoon dogs (LD: 0.05; HD: 0.04), Japanese martens (LD: 0.05; HD: 0.15), masked palm civets (LD: 0.03; HD: 0.06), wild boars (LD: 0.0; HD: 0.0), Japanese macaques (LD: 0.0; HD: 0.2), and Asian black bears (LD: 0.0; HD: 0.0).

We surveyed the dung beetle communities, including both dwellers and tunnelers, in each study site by setting one pitfall trap in each plot for three nights in June 2017. This was based on a previous study that revealed a high frequency of dung beetles in early summer (Koike et al. 2013a, b). We established nine study plots within each study site; they were at least 300 m apart to minimize or eliminate the possibility of trap interference. The plastic containers (77 mm in diameter, 96 mm in depth) containing saltwater as a preservative solution were buried to the rim in the ground, and deer dung placed inside a plastic mesh bag was suspended over the top. The dung beetles collected from each study area (species of which at least ten individuals were collected in each study area) were dried for 72 h at 60 °C, powdered and determined the nitrogen isotope ratio.

Among the dung beetles collected, we measured the δ^{15}N values in five species: *Phelotrupes auratus* (body length: 15.3 mm), *P. laevistriatus* (14.7 mm), *Onthophagus fodiens* (9.2 mm), *O. lenzii* (8.9 mm), and *C. nikkoensis* (5.7 mm). We found that in *P. auratus* (HD ($n = 6$): 2.8‰ ± 0.7‰; LD ($n = 6$): 5.1‰ ± 1.3‰, Student's t-test $P = 0.004$) and *P. laevistriatus* (HD ($n = 10$): 2.9‰ ± 0.9‰; LD ($n = 10$): 4.1‰ ± 1.6‰, Student's t-test $P = 0.049$), the δ^{15}N values were significantly lower in individuals caught in high-density (HD) areas than in those from low-density (LD) areas (Fig. 22.2). In the other three species, there were no significant differences in the δ15N values between the two study areas (*O. lenzii*: HD ($n = 10$), 4.1‰ ± 0.7‰, LD ($n = 10$), 3.0‰ ± 2.1‰, Welch's t-test $P = 0.18$; *O. fodiens*: HD ($n = 6$), 3.0‰ ± 0.8‰, LD ($n = 5$), 2.5‰ ± 1.9‰, Mann–Whitney's U test $P = 0.25$; *C. nikkoensis*: HD ($n = 10$), 2.8‰ ± 0.7‰, LD ($n = 10$), 3.2‰ ± 0.7‰, Student's t-test $P = 0.35$, Fig. 22.2).

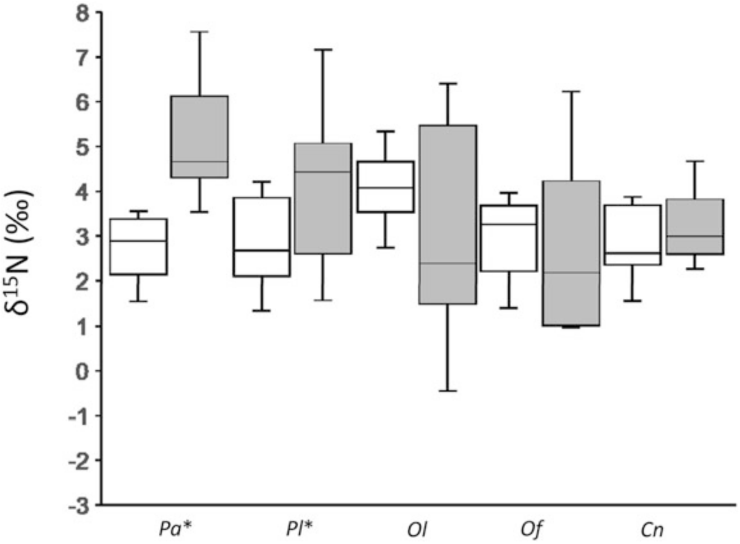

Fig. 22.2 Nitrogen isotope ratios (δ^{15}N) in the exoskeletons of dung beetles. Nitrogen isotope ratios (δ^{15}N) in the exoskeletons of *Phelotrupes auratus* (*Pa*), *Phelotrupes laevistriatus* (*Pl*), *Onthophagus lenzii* (*Ol*), *Onthophagus fodiens* (*Of*), and *Caccobius nikkoensis* (*Cn*). * Indicates the species of dung beetles that exhibited significant differences in nitrogen isotope values between the high- (white) and low-density (light gray) deer areas

It is possible that only large dung beetle species experienced the changes in their larval diets, because the δ^{15}N values of the adult exoskeleton were significantly lower in HD area than in LD area in large dung beetles only. It is possible that the high-quality feces with higher water and nitrogen contents, such as those of omnivores, preferred by large beetles decreased in availability with the increase in deer dung. In forests with increasing deer population density and declining understory, mammal feces may dry faster, potentially reducing their use by dung beetles. The drying may also potentially reduce the water content of carnivore feces and the availability of these feces to large dung beetles. However, as the population density of sika deer increased, and because the deer are gregarious (Nagata 2009), their feces were available in high density for immediate use by large dung beetles. In contrast, another large dung beetle species, *P. laevistriatus*, tended to increase in population size as the deer population density increased. This may have occurred because *P. laevistriatus* has a more diverse diet than *P. auratus*, utilizing decomposed materials other than animal feces, such as mushrooms.

Although *O. lenzii* and *O. fodiens* did not show significant differences in exoskeleton δ^{15}N values between the two study areas, there were greater variations in these values in low-deer density areas. These are relatively small dung beetle species, and their conditions to use the feces may not be as strict as those of large dung beetle species (Nichols and Gardner 2011). Therefore, in low-deer density areas, it is possible that these smaller beetles were using feces from a variety of familiar mammals, including deer; then, as the deer population density increased, the amount of usable deer feces increased, and more small dung beetles began using the easily obtained deer feces. For *C. nikkoensis*, there was no significant difference in δ*15*N values or their variation between the two study areas. It is possible that this species has more preference for deer feces.

22.4 Effect on the Ecological Function by Dung Beetle

Large herbivore overabundance can change the structure and composition of biological communities and alter the ecosystem functions that they provide. The decomposition of mammal dung is a key process in forest ecosystems that is largely performed by insects (Didham et al. 1996). Dung beetles are one of the main taxa involved in dung decomposition (Nichols et al. 2008), with both the larval and adult stages consuming the dung of other animals.

Here, we experimentally investigated how the population density of sika deer in temperate deciduous forest in Ashio–Nikko mountain area affected the decomposition of mammal dung by dung beetles, which is a key process in forest ecosystems (Iida et al. 2018). We measured a range of environmental variables (e.g., vegetation cover and soil hardness) and dung decomposition rate, measured the amount of deer dung decomposed in 1 week, and sampled dung beetles from 16 study sites with three different deer densities (high; > 15 deer/km^2 /intermediate; 6–15 deer/km^2 / low <5 deer/km^2). Then, we used a structural equation modeling to investigate the relationships between deer density, environmental variables, dung beetle biomass (classified into small or large species), and dung decomposition rate. In particular, we used path analysis to determine the causal relationships between the increase in deer abundance and dung decomposition, in which we considered several pathways (Fig. 22.3). First, the changes in the structure of the understory vegetation and soil properties due to the increase in deer density (Fig. 22.3a) would modify the habitat environments for dung beetles (Fig. 22.3b, Barbero et al. 1999; Davis et al. 2014) and that canopy openness would also influence the structure of the understory vegetation (Fig. 22.3c, Tinya et al. 2009). Second, deer density would affect dung beetle communities directly through the provision of food resources (Fig. 22.3d, Stewart 2001), and third, the alteration of dung beetle communities would influence their ability to decompose dung (Fig. 22.3e). Since the strength of these effects can vary with the body size of dung beetles (Nichols et al. 2013; Nichols and Gardner 2011), we expected that their response to the increased deer density would differ between beetles with different body sizes (Koike et al. 2014).

The results showed that the deer density had a significant negative effect on understory cover; the understory cover was significantly lower in sites with high deer density than in sites with low deer density ($p = 0.05$; Fig. 22.4). By contrast, the canopy openness had no effect on understory cover ($p = 0.55$; Fig. 22.3). Soil hardness tended to be higher in sites with high deer density than in sites with low deer density, though this was not significant (Fig. 22.3). Neither the deer density nor

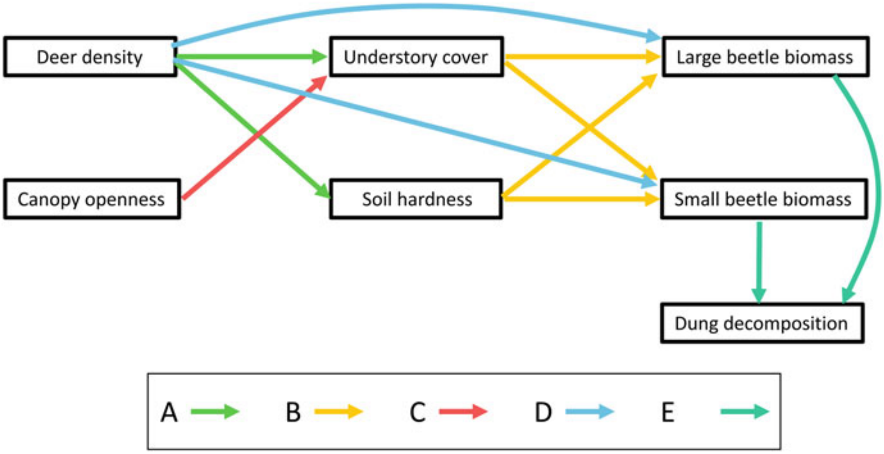

Fig. 22.3 The hypothetical model that was used to explore the effect of deer density on dung decomposition by dung beetles. Each letter (**A**–**E**) represents a possible relationship among the variables

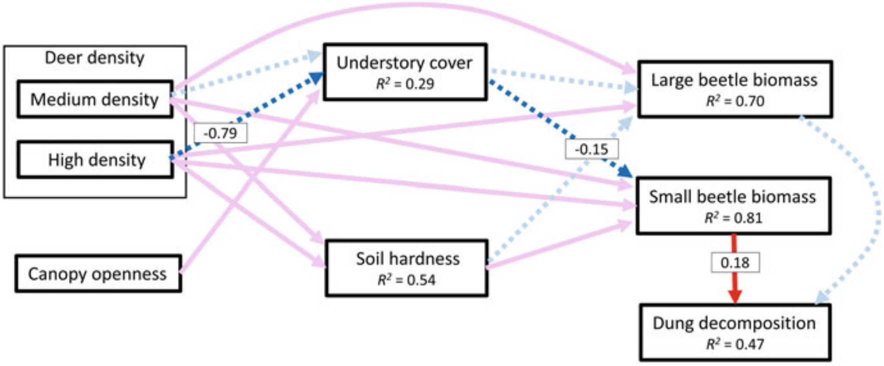

Fig. 22.4 Results of the structural equation modeling (see Iida et al. 2018 for more details about the statistical analysis). Red (solid) and blue (dashed) arrows represent positive and negative unidirectional relationships among the variables, respectively. Translucent arrows represent non-significant paths ($p > 0.05$). The standardized regression coefficients are given in the associated boxes. R^2 values for each component models are given in the response variable boxes

the soil hardness affected the biomass of dung beetles, whereas the understory cover had a significant negative effect on the biomass of small species ($p = 0.04$; Fig. 22.3). The biomass of small species had a significant positive effect on the rate of dung decomposition ($p = 0.03$; Fig. 22.3), whereas the biomass of large species did not ($p = 0.15$; Fig. 22.3).

The results show that the rate of dung decomposition increased, rather than decreased, with increasing deer density, suggesting that this alteration in ecosystem functions was induced by the changes in the structure of dung beetle communities (i.e., the increase in the population of small dung beetles). In fact, this study found that the biomass of small-bodied species increased with increasing deer density, whereas that of large-bodied species was not affected by the deer density. Furthermore, the dung decomposition rate was positively related to the biomass of small-bodied species but unrelated to that of large-bodied species. Overall, these results show that the increase in deer density affects the decomposition rate of mammal dung by changing the structure of dung beetle communities.

22.5 Conclusion

A series of studies on the relationship between deer density and dung beetles revealed that the response of dung beetles to the changes in deer density is highly complex and has effects on ecosystems and ecosystem functions through cascade effects. However, these effects are expected to be greatly influenced by the duration of high deer densities and differences in mammal fauna in each region. Therefore, in order to clarify these impacts, it is necessary to identify them in each area with certainty. Thus, the understanding of how large herbivore overabundance affects each ecosystem member or ecosystem functions is important to evaluate the ecological consequences of their overabundance and ultimately manage their populations appropriately.

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Chapter 23
Impact of Sika Deer on Soil Properties and Erosion

Takashi Gomi, Mitsuru Oohira, Marino Hiraoka, Shusuke Miyata, and Yoshimi Uchiyama

Abstract Ground cover by understory vegetation and litter is one of key factors for mitigating soil erosion as well as for maintaining soil properties as an ecosystem function. Reduction of understory vegetation by the overpopulation of deer can elevate the rate of soil erosion due to rain splash and overland flow. Changes in surface soil conditions also occur in soil properties including bulk density, particle size distribution, and organic matter contents. Furthermore, soil erosion on hillslope can affect in-channel sediment transport of headwater catchments, because of tight linkages between hillslopes to streams at incised valleys. Thus, catchment scale conservation needs to be established for mitigating the effects of deer overpopulations on occurrence of surface runoff and soil erosion and consequent changes in sediment dynamics and water quality in downstream. This chapter will explore how changes in vegetation cover by deer affect hydrologic and geomorphic processes related to the soil at scales of hillslopes and headwater catchment scales.

T. Gomi (✉) · M. Oohira
Graduate School of Agriculture, Tokyo University of Agriculture and Technology, Fuchu, Japan
e-mail: gomit@cc.tuat.ac.jp

M. Hiraoka
Erosion and Sediment Control Research Group, Public Works Research Institute, Tsukuba, Japan
e-mail: hiraoka-m573bt@pwri.go.jp

S. Miyata
Disaster Prevention Research Institute, Kyoto University, Takayama, Japan
e-mail: miyata.shusuke.2e@kyoto-u.ac.jp

Y. Uchiyama
Natural Environment Conservation Center, Kanagawa Prefecture, Atsugi, Japan
e-mail: uchiyama.vka1@pref.kanagawa.lg.jp

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23.1 Introduction

The increase in deer population in mountain headwater catchments alters changes in vegetation ground cover in mountainous areas at various scales (Sakai et al. 2012; Ohashi et al. 2014). Such changes in understory vegetation cover alter soil physical properties due to soil erosion and loss of mineral and organic soils by changes in hydrogeomorphic processes (Suzuki et al. 2008). Furthermore, recent studies showed that vegetation cover is also declined due to not only the overabundance of deer population but also lack of radiation input to forest floor for the growth of vegetation in dense planted forests (Onda et al. 2010; Suzuki and Ito 2014). Thus, both wildlife management and forest management (e.g., thinning) are strongly linked to the conservation of water and soil in mountainous regions.

Headwater catchments (approximately with area of 1km^2 and less) are a key management unit with respect to soil and water conservation (Gomi et al. 2002; Fig. 23.1). Because headwater catchments are an important source of water, sediment, and nutrient to downstream within large watershed contents, conditions and distribution of understory vegetation are important indicators for understanding water and soil dynamics and resultant changes in water quality. Although the areas of headwater catchments are rather small, numerous headwaters in upstream can contribute flux of materials to downstream with large watershed contents (Gomi et al. 2002). Thus, various stakeholders within large watersheds are concerned about the deterioration of the natural environment due to reducing vegetation ground covers and increases in soil erosion in headwater areas. Furthermore, maintaining

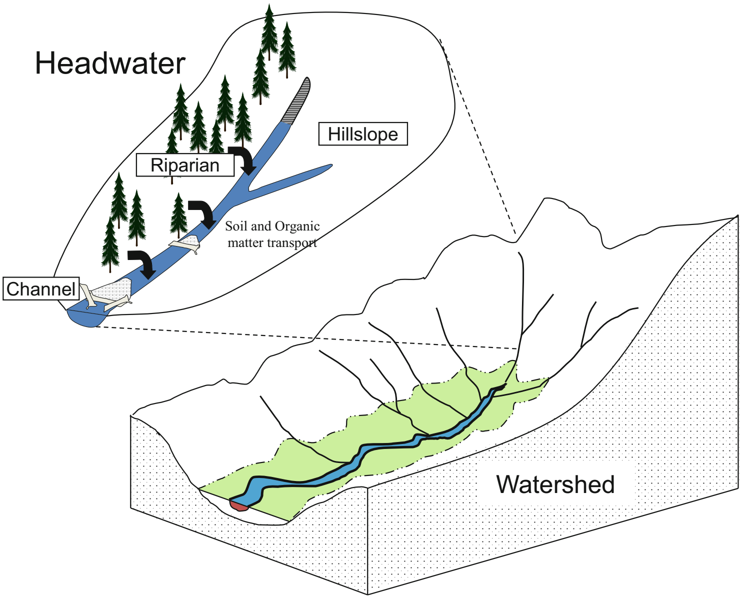

Fig. 23.1 Schematic illustration of headwater catchments within large watershed

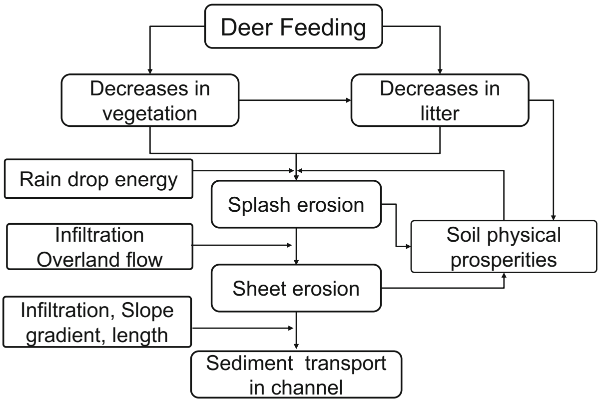

Fig. 23.2 Flow diagram of deer overpopulation to soil erosion and sediment transport

understory vegetation for water and soil conservation is one of the key factors for forest as "green infrastructure" in mountainous regions (Nakamura et al. 2020). In these contexts, catchment-scale analysis of deer overpopulation on hillslope and stream ecosystems with respect to hydrologic and geomorphic processes is essential (Sakai 2013).

Soil erosion is associated with interactions among various factors including rainfall, soil conditions, topographic factors (slope length and gradient), a surface condition such as vegetation, and litter covers (Fig. 23.2). Thus, in this chapter, we firstly summarize the characteristics of forest soils and hydrological processes in forested hillslope and watersheds. Then, we secondarily demonstrate the effects of deer overpopulation and decreases in vegetation ground cover on hydrological processes and soil erosion, particularly focusing on headwater catchments. Finally, we show an example of catchment-scale monitoring for evaluating the changes in linkages between hillslopes to channels associated with deer overpopulation and vegetation changes.

23.2 Hydrological Processes and Soil Conditions in Forested Landscape

Hydrological processes in forested environments are diverse depending on the characteristics of forest stand conditions, understory vegetation, and soil physical properties. Rainfall on forested area can be intercepted by forest canopy before reaching to forest floor (Hewlett 1982) (Fig. 23.3). Intercepted rainfall will be partitioned into throughfall (raindrop under forest canopy) and stem flow. Approximately, 70–80% of rainfall became throughfall and 5–10% of precipitation become stem flow, depending on the tree stand condition (density, species, and leaf area index) (Chang 2006). Part of the throughfall will also be intercepted by understory vegetations such as herbaceous plant and/or shrubs. Once water reaches to soil

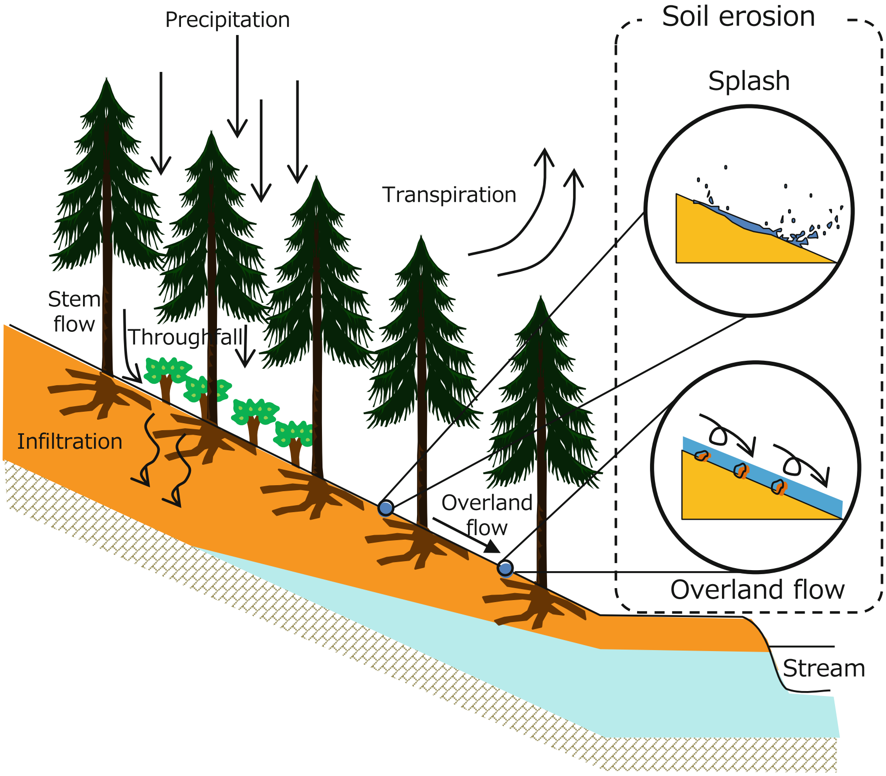

Fig. 23.3 Hydrological processes and soil erosion on hillslope

surface, water can be percolated into soil matrix depending on infiltration capacity of soil surface. In general, infiltration capacity of soil surface in forested hillslope is high enough for all water to percolate into soil, because of high porous soil with litter cover and available organic matter (Hewlett 1982).

When mineral soil surface is exposed because of the reduction of understory vegetation and litter, infiltration capacity becomes low and induces infiltration-excess overland flow (e.g., Hortonian overland flow; Dunne and Dietrich 1980). In particular, when raindrops fall and hit the soil surface, the energy of their fall destroys the soil surface structure (Kinnell 2005). Soil is composed of an aggregate of fine particles, but raindrops destroy the aggregate structure and bounce up soil particles and organic matter. The splashed fine soil particles clog the soil surface and form a thin layer (crust layer) that is difficult for water to penetrate (Moore and Singer 1990). In general, raindrop particle under the forest canopy is greater than that in outside forest and resultant raindrop kinetic energy is high under the forest canopy (Nanko et al. 2004). Soil water repellency also affects the infiltration capacity in certain forest conditions such as cypress plantations (Gomi et al. 2010). Using an experimental rainfall simulator, Hiraoka et al. (2010) confirmed that soil infiltration capacity on bare slopes was about 20 mm/h, while ones on understory vegetation cover became 100–300 mm/h. Thus, on slopes with reduced infiltration capacity due to soil surface conditions, rainwater that does not fully infiltrate into the soil and surface flow likely mobilized as surface runoff.

Once infiltration excess occurs, water can be accumulated on the soil surface and ponded on micro-topographic depression. After such micro-topographic depression is filled by water on the hillslope, surface water can be mobilized as overland flow toward downslope. The overland flow will be continued to hillslope to the channel depending on the continuity of flow (Gomi et al. 2008). In general, soil on forested land is highly heterogeneous, and continuous overland flow really occurs, despite high and intense periods. Thus, the intensity of rainfall is also one of the important controlling factors for the occurrence of surface runoff in a forested hillslope.

23.3 Soil Erosion and Effects of Deer Overpopulation on Forested Hillslopes

Main types of erosion that occur on forest slopes in a temperate climate can be categorized into those caused by direct rainfall and surface flow during the rainfall period. Raindrops from rainfall cause raindrop erosion, in which the falling energy destroys the structure of the soil surface and bounces up soil particles and organic matter (Fig. 23.3). Surface runoff erosion can be broadly classified into sheet erosion, rill erosion, and gully erosion (Morgan 2009). On forest slopes, splash and sheet erosion can be the main factors for changes in soil erosion. Rainfall intensity typically associates with splash erosion because high and intense precipitation indued high kinetic energy for detaching soil surface (Nanko et al. 2008). Sheet erosion by surface runoff also occurred on the forested hillslope, while the runout distance of overland flow is generally short due to rough and heterogeneous surface (Gomi et al. 2008). Hence, once surface runoff water is concentrated at micro-topographic depress and concave topography, development of rill and gully may occur.

Erosion due to freezing and thawing also occurs when water in the soil freezes during the cold night, lifting the soil (frost columns) and thawing due to rising temperatures and solar radiation during the day, destabilizing it (Ferrick and Gatto 2005). Freezing of soil surface also associates with soil surface cover by litter and understory vegetation. Freezing and thawing also produce large particle soil, including gravel and cobbles, while rain splash erosion produces rather small particles such as clay and sands (Imaizumi et al. 2019).

Soil erosion is less likely to occur on forest slopes where forest floor vegetation and deciduous leaves exist, but soil erosion has become more apparent due to the decline of understory vegetation covers. This leads to soil erosion by raindrops and surface currents. In a study of bare cypress forest slopes, it was reported that there was a 4.5-fold difference in soil erosion between forest floor slopes and vegetated

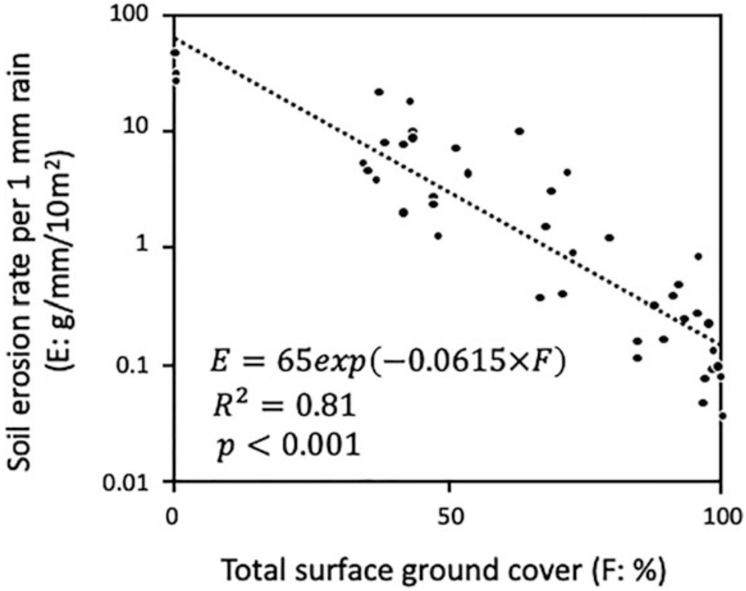

Fig. 23.4 Relationship ground cover and soil erosion (after Chu et al. 2010)

slopes (Miyata et al. 2009). Along with the decline of dwarf bamboo due to deer feeding, the impact on the diversity of vegetation species due to the priority of resistant and non-preferred species has also been pointed out (Tamura and Yamane 2017). By the experimental removal of vegetation covers (including dwarf bamboo), total amount of soil and litter in vegetated plots was about 1.2- to 3-folds greater than in the ones in plots with vegetation removal (Furusawa et al. 2003).

Based on plot measurement with 5 m long and 2 m wide affected by deer overpopulation in Tanzawa mountain, Chu et al. (2010) found that negative correlation is expressed by an exponential function [$E = 65\ \exp.\ (-0.0615 \times F)$] between the amount of the soil erosion per mm of the rainfall (E) and the forest floor cover percentage (F) (Fig. 23.4). This result suggested that small changes in ground cover induces large changes in soil erosion. Based on a detailed investigation of splash and sheet erosion, Ghahramani et al. (2011a, b) found that splash contribution to the sediment transport was highly varied with greatest variability at plots with sparse ground cover. Biligetu et al. (2013) found that surface runoff and rainfall intensity strongly affect sheet erosion because of the combination of detachment and transport.

23.4 Vegetation-Soil Interaction for Soil Conditions and Deer Effects

Seasonal changes in litter and vegetation cover are important indicators for understanding the superstability of soil erosion. Hiraoka et al. (2013) evaluated seasonal changes in forest floor cover percentage (total percent cover of understory vegetation and litter) using interval cameras. Seasonal variation in the cover percentage of litter was associated with precipitation during typhoon events and decline in daily air temperature and species composition of overstory trees. Soil surface cover varied from 30 to 90% by seasons because of the movement of litters. Furthermore, they also confirmed that, when daily air temperature fluctuated around 0 °C, surface soil creep occurred from freezing and thawing with sparse litter cover. Thus, seasonal dynamics of ground covers can be assassinated to biological processes for providing litter and physical processes for the mobility of litters.

Deer overpopulations alter soil physical properties via changes in vegetation and litter. For instance, Harada et al. (2020) showed that deer density decreased in the litter layer and increased bulk density and porosity. Changes in soil properties and occurrence of soil erosion related to the availability and types of litters. By comparing to Japanese cypress, cedar, and broad-leaved forest in areas affected by deer overpopulation, Yanagi et al. (2008) showed soil erosion was more pronounced at hillslope with Japanese cypress forest because litter of Japanese cypress is rather small and easy to be mobilized by splash and sheet erosion (Miyata et al. 2009). Previous studies often describe the relationship with aboveground biomass as a water-soil conservation effect, but the rhizome layer is also highly important in terms of directly changing soil physical properties (Shinohara et al. 2016). Future research on the water-soil conservation function related to deer overpopulation should be related to “forest soils” from the perspective of biodiversity and ecosystem services in forest ecosystems. In recent years, attempts have been made to induce single- to multi-storied forests, and it is expected that the multi-storied structure on the ground, from tall trees to forest floor vegetation, will result in a multi-storied structure in the soil. The diversity of vegetation species is also known to increase the aboveground biomass, and this aboveground change is also expected to affect the rhizome biomass (Liira and Zobel 2000). From this point, species composition but not vegetation cover of understory vegetation should be monitored because vegetation cover of understory vegetation may be high by the dominance of single unpalatable or browsing tolerant species even under high density of deer species (Ando et al. 2006; Tanentzap et al. 2012).

Soil erosion also alters the qualitative conditions of soil due to the loss of carbon and nitrogen (Pimentel et al. 1995). The accumulation of carbon and nitrogen in soils is a product of material cycling over long-term scales; hence when soil erosion occurs at a rate shorter than the rate of soil formation, carbon and nitrogen in the soil are also lost (Furusawa et al. 2011; Teramage et al. 2013). Soil erosion and loss of soil also reduce the availability of seeds in the soil matrix (Tamura 2020). Long-term loss of soil nutrient and seeds likely reduce the resilience of recovery after the manipulation of deer. Furthermore, soil degradation affects the assessment of soil carbon stocks, which is important processes for estimating carbo flux for evaluating global warming. Furthermore, changes in soil conditions can be propagated to the changes in the macroinvertebrate community in soil (Saitoh et al. 2008). However, very few research examples for comprehensive analysis for quantitative evaluation of soil physical and biological processes related to deer overpopulation.

23.5 Importance of Watershed Approaches

Although various studies demonstrated the effects of deer overpopulation on vegetation ground cover and soil erosion, catchment-scale analysis for evaluating the effects of deer overpopulation on hydrologic, geomorphic, and biological processes is relatively rare. Nature and degree of linkages between hillslope and channels are important aspects for how changes in the landscape can propagate (or not propagate) downstream (Gomi et al. 2002) (Fig. 23.1). The degree of linkage varies spatially and temporally due to topographic aspects and the distribution of vegetations and litters. In addition, temporal changes in soil surface conditions by vegetations and litter (e.g., Hiraoka et al. 2013) likely affect the degree of connection between hillslope to headwater channels. Depending on the connectivity from hillslope sources of sediment, mobility of bedload sediment (Gomi and Sidle 2003) and concentration of suspended sediment load (Gomi et al. 2005) also differ.

For investigating the changes in the ground cover condition by deer overpopulation, one of the approaches is a catchment-scale experiment by excluding deer for entire watersheds. One example for this experiment was conducted by Ashiu Experimental Forest by Kyoto University (Sakai et al. 2012, 2013; Sakai 2013; Chap. 27). Sakai et al. (2012) showed that recovery of understory vegetation due to the exclusion of deer browsing indirectly alters aquatic insect assemblages by changes in sediment runoff and subsequent sandy sedimentation of the streambed. This study confirmed the strong linkages of hillslope soil erosional processes to in-channel sediment dynamics. Nakagawa (2019) further demonstrated the effects of catchment-scale hydrogeomorphic processes by deer overpopulation related to fish populations downstream. We will show detailed catchment-scale monitoring by using deer exclusion in mountainous headwaters.

Catchment-scale observation can also be essential for identifying long-term recovery processes after the management of deer. For instance, Tanentzap et al. (2009) showed full recovery of vegetations after deer manipulation required 10–20 years. Such long-term recovery of vegetations is possibly associated with long durations of deer impacts on vegetation and soil conditions (Tanentzap et al. 2012). In general, deer fence with certain plots (e.g., 10 × 10 m) was applied to investigate deer manipulation on vegetation recovery (Tamura and Yamane 2017; Tamura 2020). Availability of seeds in the soil can vary depending on topography and positions within catchments, likely altering the recovery (Tamura 2019). Catchment-scale exclusion can examine the spatial variability of recovery of deer manipulation and its controlling factors within heterogeneous landscape conditions.

23.6 Watershed Scale of Field Monitoring

23.6.1 Outline of Monitoring Headwaters

We demonstrate the examples of catchment-scale monitoring from hillslope to headwater streams in catchments where understory vegetation was heavily degraded by deer overpopulation. We conducted catchment-scale monitoring in the Ohorasawa experimental watershed (58 ha catchment area) located in the upper reaches of the Nakatsu River of the Sagami River system in the eastern Tanzawa Mountains. The elevation of this area ranges from 432 to 878 m above sea level. The geology belongs to sedimentary rocks. Dominant overstory vegetation is Japanese cedar (*Cryptomeria japonica*) and cypress (*Chamaecyparis obtusa*) and deciduous broad-leaved forests. As a result of long-term deer herbivory, unpalatable for deer or tolerant plant species to deer browsing such as *Boenninghausenia japonica* became dominant.

The primal objective of this catchment study is to assess characteristics of water and sediment runoff in a deer-impacted watershed, understand the changes in water and sediment runoff through recovering understory vegetation, and examine the effectiveness of the management practice. Two adjacent small tributaries were selected as the manipulated watershed (No. 3: 7 ha) and the control watershed (No. 4: 5 ha), respectively, in order to examine the effectiveness of herbivory control using the paired catchment method. At the catchment outlets, weirs to observe runoff and sediment transport were established in 2009 (Fig. 23.5). Then, at the end of 2011, a deer-excluded fence was installed in basin No. 3 to prevent deer browsing in the whole watershed (Fig. 23.6). This method is called the Before-After Control-Impact (BACI) experiment method. BACI method can detect the magnitude of changes in external pressure on the natural environment and identify the factors that determine the magnitude of the impact (Smith et al. 1993).

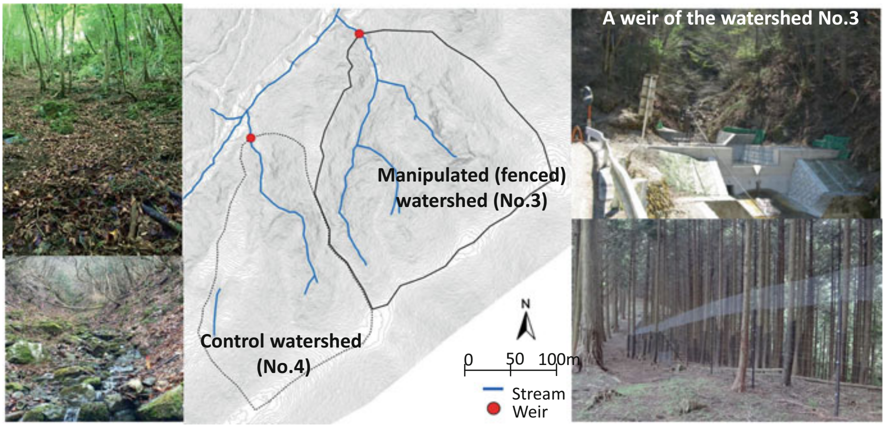

Fig. 23.5 Monitoring headwater catchment for hillslopes and streams

Class1（Bare surface） Class 2（Small litter cover） Class 3（Full Litter cover）

Class 4
（Vegetation cover < 40%）

Class 5
（Vegetation cover 40~80%）

Class 6
（Vegegation cover > 80%）

Fig. 23.6 Vegetation ground cover classification

We describe the distribution of understory vegetation and runoff of suspended sediment (fine sediment that floats in the water) and bedload sediment (coarse sediment that is moved near the stream bed by flowing water). Based on these findings, we will illustrate characteristics of sediment transport from deer-impacted watersheds and discuss the potential recovery processes.

23.6.2 Spatial Distribution of Understory Vegetation and Soil Erosion

We surveyed to understand the distribution of understory vegetation in the whole watershed No. 3 and No. 4. Fifty-eight 50 × 50 cm quadrats were distributed along several transects from the valley to the ridge, and the amount of litter and plant cover was measured in six levels: (1) bare ground, (2) small amount of litter cover only, (3) full litter cover, (4) vegetation cover less than 40%, (5) vegetation cover 40–80%, and (6) vegetation cover more than 80% (Fig. 23.6). Based on this classification, the forest floor in watersheds was classified into the following six classes. Further, we assessed plant biomass of the understory vegetation and canopy openness above the plot.

A spatial distribution map of the land surface cover based on field investigation was created by interpolation using ArcGIS (Fig. 23.7). The areas of unvegetated (classes 1–3) hillslopes were larger in watershed No. 3 than in No. 4. The

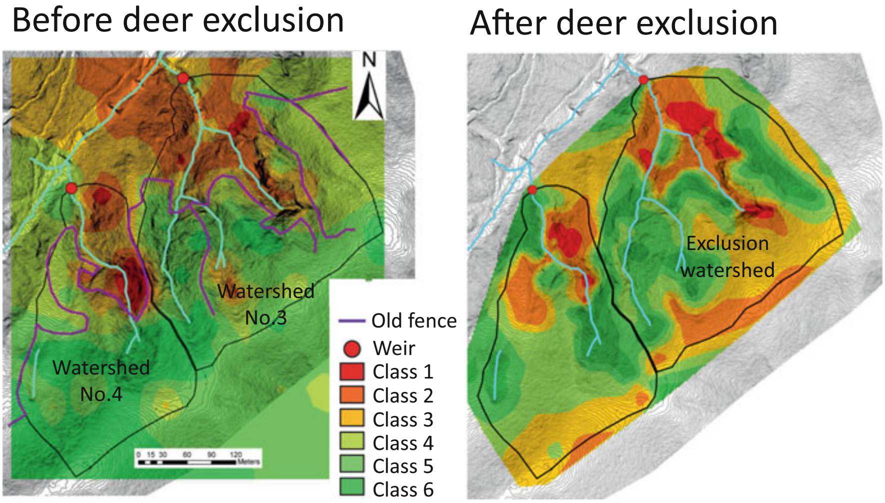

Fig. 23.7 Changes in ground cover before and after deer exclusion

unvegetated areas were distributed on the steep hillslopes along the stream channels. The average biomass of understory plants in classes 1–6 was 2.0 g, 1.4 g, 1.8 g, 16.7 g, 45.0 g, and 95.5 g, respectively. Those biomasses tended to increase as the total cover ratio increased. The average canopy openness was about 4% at cover classes 1–3, with no understory vegetation. In vegetated plots, the canopy openness of classes 4–6 are 5.4%, 6.9%, and 12.8%, respectively, indicating that the canopy openness contributed to form vegetation cover (Gomi et al. 2012). The dominant plant species were *B. japonica*, *Oplismenus undulatifolius*, and *Leucosceptrum japonicum*; those were unpalatable or tolerant herbaceous plants.

23.6.3 Changes After Installation of Deer Exclosure

The areas of bare soil surface as the source of sediment production were almost three times larger in catchment No. 3 than in catchment No. 4. The main source of sediment production was thought to be the area around the stream channel, where the large bare ground surface was distributed. The transported distance of gravels in the stream channel also tended to be greater in catchment No. 3 than in catchment No. 4. These differences in the distribution of production sources and sediment transport in the channel have increased the runoff of suspended and bedload sediment from the catchment. The results suggest that hillslope coverage, hillslope sediment production, and sediment transport processes in the stream channel are keys for understanding the effects of deer-induced decline of understory vegetation and the future vegetation recovery on sediment discharge from the catchment.

The survey of understory vegetation in 2018 after catchment-scale deer exclusion showed that the lower hillslope areas along the stream channel remained widely not vegetated, and vegetation recovery was limited. Four observation plots on bare hillslopes continued to produce 0.8 to 3.6 t ha^{-1} year^{-1} of sediment from 2010 to 2017. In addition, catchment No. 3 has been producing from 0.1 to 15.4 t ha^{-1} year^{-1} (average 3.7 t ha^{-1} year^{-1}) of bedload sediment in the observations from 2012 to 2018. This sediment transport rate is relatively high compared to natural conditions (Gomi and Sidle 2003; Hiraoka et al. 2015). These monitoring results indicated that the amount of sediment runoff had not been decreased even after the installation of the enclosure for 6 years. Because major source areas of sediment near channels and at riparian zones had remained as bare land, 6 to 8 years after exclusion appeared to be not enough for detecting the changes in sediment transport.

A survey of the understory vegetation in 2018 showed a partial recovery from the upper hillslopes to the ridge in catchment No. 3. In addition, even in the area where palatable and intolerant plant species have recovered, the growth of shrub such as *Rubus palmatus* var. *coptophyllus* and *Deutzia scabra* is observed. However, the frequency of tree species forming overstory is low, indicating that forest successions are still slow. Those conditions suggest that the impact of past foraging on vegetation is continuing 8 years after installing the exclosure. The similar phenomenon was observed in Hokkaido, northern part of Japan (Uno et al. 2019). Because soil properties and availability of seed is important for recovery (Harada et al. 2020), spatially heterogeneous topography and seed sources alter the recovery processes (Côté et al. 2004; Tanentzap et al. 2012). Therefore, it is necessary to evaluate ecosystems and recover their functions with long-term succession based on ecological resilience.

Further, because of growth of abandoned plantation coniferous forests, the canopy tends to close, and understory vegetation cover is declining in such areas. Therefore, to reduce sediment runoff by restoring understory vegetation on the forest floor, forest management such as thinning is needed. In addition, at hillslopes and along riparian zone, a temporal engineering approach for controlling soil surface erosion is possibly applied for inducing the colonization of understory plants. Therefore, to achieve the reduction of sediment runoff, it may be necessary to take comprehensive restoration practices in watershed scale, and researches are currently being conducted from this perspective.

23.7 Conclusions

As described above, the importance of forest floor vegetation and the deciduous layer in forest ecosystems has been reaffirmed by the emergence of forest soil erosion along with the problems of degradation of deer damage. For forest management such as cutting and thinning, understory vegetation typically grows quickly. Hence, once after the growth of understory vegetation, forest floor vegetation that has increased due to these operations has also become food for new deer, which have been eating away at it (Iijima and Otsu 2018). It is no exaggeration to say that the success or failure of forest floor vegetation recovery aimed at restoring the water and soil conservation functions of forests depends on conservation of soil through integrated management of forests and wildlife.

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Chapter 24

Responses of Ground-Layer Vegetation and Soil Properties to Increased Population Density of Sika Deer and Environmental Conditions

Maki Suzuki

Abstract Forest ecosystems change as the population of sika deer increases along with expanding habitat range. The trajectory of the change is of interest to ecologists and forest managers. Here I present the results of a natural experiment in a warm-temperate forest, with the aim of showing how vegetation and soil properties of forests change according to the increase in the population of sika deer (*Cervus nippon*). At our study site, ground vegetation rapidly decreased as the deer population density increased, whereas vegetative species richness showed a hump-shaped pattern. The damage to vegetation seemed to have accumulated belowground and resulted in further decreases of ground vegetation and soil compaction, as evidenced in a follow-up study 11 years later. The recovery of vegetation was minor, even in areas where deer density had decreased. These pronounced and long-lasting impacts of sika deer on forest vegetation are partly attributable to the high herbivory pressure caused by this species, but the low productivity of the dark forest floor also seems to play a role.

24.1 Introduction: Forest Vegetation and Disturbance by Sika Deer—A General Perspective

The resilience of ecosystems subject to disturbance is a classic subject in ecology studies. Many studies on this topic have demonstrated that ecosystem resilience is dependent on productivity and the intensity and frequency of disturbance, as well as the pre-disturbance history of the ecosystem (Young et al. 2001). The response of ecosystems to herbivory pressure has also been discussed in this context. Herbivory pressure is a low-intensity and high-frequency disturbance compared to other

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M. Suzuki (✉)
Department of Natural Environmental Studies, Graduate School of Frontier Sciences, The University of Tokyo, Kashiwa, Japan
e-mail: suzukima@edu.k.u-tokyo.ac.jp

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disturbances, such as lava flows, landslides, and accidental fires. The weak and frequent disturbance of herbivory, together with environmental productivity, tend to cause complex reactions of ecosystems. This complex reaction has been the focus of numerous studies, especially in grassland-livestock systems (e.g., Augustine and McNaughton 1998; Olff and Ritchie 1998). However, findings from grassland studies cannot be directly applied to forest ecosystems, where the combined effects of trees and cervids, both of which are ecosystem engineers, can completely change the system properties in relatively short periods. In extreme cases, forests can be transformed into grassland or scrub that persist long afterward (Stromayer and Warren 1997). Such drastic examples have prompted researchers to pose important questions related to deforestation, a global issue of this century. To what extent are forests tolerant or resilient to the impacts caused by deer? Do forests autonomously recover from the damages caused by deer? The answers to these questions will depend on the history of the ecosystem, climatic conditions, and internal factors, such as tree species, and the behavioral character and population density of the deer species as a disturbance factor.

Before discussing the case of sika deer (*Cervus nippon*), it is worth reviewing the factors that influence the degree of tolerance or resilience of an ecosystem against herbivory pressure. A theoretical model derived from grassland-livestock systems predicts the diversity of plant species based on the grazing intensity and soil moisture (Milchunas et al. 1988) or, in a more generalized context, the environmental productivity (Cingolani et al. 2005). According to this model, the diversity of plant species in a semiarid (less productive) grassland follows a simple decreasing trend with grazing intensity; whereas in a subhumid grassland with intermediate productivity, the species richness shows a hump-shaped pattern with grazing intensity, as is expected by the intermediate disturbance hypothesis (Connell 1978). This model was an extension of a general model on the relationships between species diversity, environmental productivity, and disturbance (the dynamic equilibrium model: Huston 1979). To apply Huston's model to grazing systems, Milchunas et al. (1988) included another important factor into their model: the history of grazing. According to their model, plant species that evolved under high grazing intensity necessarily show higher tolerance and/or resilience to herbivory compared to species that evolved under low grazing intensity, and this affects the response of species diversity to grazing intensity in each ecosystem. In summary, the resilience of an ecosystem to herbivory pressure is expected to depend on the intensity and frequency of herbivory, as well as the history of herbivory in that ecosystem.

The response of forest ecosystems to herbivory by sika deer may be understood in the above context, although a few system-specific features should be noted. First, because the diet of the sika deer is quite broad, the deer can exert a variety of effects on the ecosystem (Gill 1992). Browsers, such as most deer species, tend to eat the young shoots of saplings and seedlings, which decreases the recruitment potential of canopy trees (Gill 1992). Grazers (e.g., livestock such as sheep and cattle) tend to damage the ground vegetation and tree seedlings too, when the density of grazing animals is high (Putman 1996). Because sika deer are both browsers and grazers, they cause damage to the ground vegetation as well as emerging trees (Takatsuki

2009). Surprisingly, sika deer are known to eat even leaf litter on the forest floor to survive a food shortage (Takahashi and Kaji 2001). Moreover, natural regulation of sika deer population is unlikely under the weak density dependence of this species (Kaji et al. 2010). Thus, overconsumption by sika deer can result in a remarkably strong influence on forest vegetation.

Secondly, large herbivores sometimes affect the conditions of the leaf litter and topsoil, which may further cause indirect effects on plant growth, either in supportive or inhibitory directions. There have been many reports of herbivory-mediated changes in vegetation affecting the litter quality and, consequently, the decomposition process (Carline et al. 2005; Pastor et al. 1993; Sankaran and Augustine 2004; Stark et al. 2010). Such changes in the decomposition process, either acceleration or deceleration, sometimes trigger a feedback reaction among the vegetation and the belowground system (Kardol et al. 2014; Singer and Schoenecker 2003). There are also reports of deer-mediated physical changes of the forest soil, such as low porosity and high bulk density (Gass and Binkley 2011; Heckel et al. 2010; Wardle et al. 2001), and consequent loss of water permeability and water potential (Furusawa et al. 2001). However, it is not clear to what extent these various findings are applicable to the sika deer-forest system. Topsoil compaction (decreased porosity and increased bulk density) is frequently observed in forests with dense populations of sika deer (Gass and Binkley 2011; Heckel et al. 2010; Wardle et al. 2001), but the soil chemical condition and decomposition process in these systems have rarely been observed. In one study, an experimentally increased deer population density did decrease ground vegetation and decreased the abundance of soil microorganisms, but no change was seen in the decomposition rate (Niwa et al. 2011). No feedback path has been reported between soil condition and vegetation pattern, as triggered by sika deer. These facts suggest a buffering mechanism that mitigates the impact of the deer population on the forest system. However, we still cannot conclude that sika deer do not cause any indirect impacts on vegetation through underground mechanisms.

Lastly, the local history of the forests and sika deer population may affect the reaction of a forest to the impact of sika deer, possibly causing the differences found between European and East-Asian forests. European forests have very limited experience of disturbance caused by sika deer that were introduced as game animals from East Asia a century ago (Chap. 29). The resilience of European forests to damage caused by sika deer may depend on whether these forests had large herbivores with similar behavior to that of sika deer. On the other hand, the resilience of Japanese forests may be affected by another historical factor. Since prehistoric times, much of the land in Japan had been covered by woodlands, grasslands, and slash-and-burn fields, all managed for daily use (except on Hokkaido, on some islands, and in high elevation areas). For the most part, sika deer are believed to have lived in such semi-natural landscapes for long periods. However, with the rapid modernization in the late nineteenth century, hunting (culling) pressure increased, and the habitat of sika deer was reduced, resulting in the decrease of many local populations of sika deer to the point of near extinction. The situation changed again in the 1960s, with rapid economic growth and the “fuel revolution,” which replaced wood with fossil fuels. With these very significant changes in society, foraging for firewood and other natural commodities practically ceased, and, consequently, most of the semi-natural lands were abandoned (Oono et al. 2020). Some of these lands have been transformed into conifer plantations for wood production (Yamaura et al. 2012). The remaining woodlands gradually matured as secondary forests; they now have the appearance of purely natural stands. As a result of these drastic changes, forest areas currently occupy approximately 70% of the Japanese land. The same socioeconomic changes have resulted in the gradual rehabilitation of most local populations of sika deer since the 1970s, to the point that the deer have now become overabundant. The current generation of sika deer inhabits matured forests grown in the previous decades when the deer populations were at their lowest. These newly established forests and vegetation have not until now experienced such high deer density; thus, these forests might not have the resilience to withstand the impact of a growing deer population.

We studied the response of forest vegetation to an overabundance of sika deer, with a research focus on the three points we have just discussed. The Boso Peninsula, where the study site is located, has many advantages in terms of study design; however, the low diversity of forest types in the peninsula limits our discussion to warm-temperate evergreen forests. The results of the study may not be applicable to other forest types, such as cool-temperate forests (see Chaps. 20 and 26) and subtropical forests (see Chap. 19), where the productivity and function of forests are different from those of our study site. Nevertheless, our system is unique in terms of the natural density gradient of the sika deer population, which lends itself to a useful study of forest resilience to deer impact.

24.2 Deterioration of Ground Vegetation as Deer Population Density Increases

The Boso Peninsula (35.4°N, 140.1°E), only 50 km from the capital, extends 60 km east-west and 70 km north-south. Due to the warm current in the Pacific, the climatic conditions are warm and mesic; in 2019, the mean, maximum, and minimum temperatures were 16.6, 35.5, and − 1.7 °C, respectively, and the annual rainfall was 2255 mm (at the Kamogawa climate station of Japan Meteorological Agency). The vegetation class of the peninsula is warm-temperate. Agriculture, fishery, and tourism are major industries in the southern part of the peninsula. Forests and woodlands occupy more than half of the hillside area—mostly plantations of evergreen conifers (Japanese cedar *Cryptomeria japonica* or Japanese cypress *Chamaecyparis obtusa*) or broad-leaved forests at the late-successional stages. Farmland expands in the lowland area and narrow intermountain plains, where there has been serious damage by sika deer.

The forest regions that sika deer inhabit are not primeval forests but have long been affected by anthropogenic disturbances. Until the early twentieth century, these forests were mainly coppice woodlands, in which the local inhabitants collected firewood as well as leaf litter as fertilizer for farmlands and practiced slash-and-burn farming. After these activities largely ceased in the 1950s–1970s, some of these forests were transformed to conifer plantations, and others became secondary forests through natural succession. These secondary forests have since matured and have dense closed canopies and dark forest floor. Conifer plantations also show closed canopies and dark forest floor due to the relative inactivity of the foresters who have faced financial difficulties. The darkness of the forest floor at least partly explains many ecological and management problems, which will be discussed later. These two forest types, conifer plantations and secondary forests, are fairly common across the Japanese warm-temperate region, and thus the study in this peninsula can be a case study with broad applicability.

The sika deer population in the Boso Peninsula is spatially and genetically separated from the mainland population. The range of the population in the peninsula has gradually shrunk from the late Edo era (nineteenth century) due to culling and habitat distraction. According to a rough estimation reported in 1974, approximately 500 deer remained on the peninsula, restricted to a narrow range in the southeastern region (Chiba Prefecture 2004). Afterward, the sika deer in the Boso Peninsula gradually recovered their lost territory. The territory is still expanding but at this time (2021) remains separate from that of the mainland population.

The monitoring of the Boso Peninsula population was launched in the early 1990s; the current monitoring system of density distribution was established in 1996. The monitoring method is based on fecal pellet counting. In this method, technicians walk along lines, 1 km in length, that have been set across the peninsula at a spacing of 3–5 km and count all deer fecal pellets seen. Based on this data, the local government can roughly estimate the population level for each monitoring route. Some of these monitoring routes are close to monitoring sites where the population density is estimated by direct counting; i.e., the block count method (Maruyama and Nakama 1983). This method provides for a more accurate estimation of the size of the deer herd: a regression line is drawn between the observed herd of deer and the fecal density measured near the monitoring route. By applying this regression model to the records of fecal pellet sampling, the spatial distribution of deer density across the peninsula can be roughly estimated (Note: a more complex estimation, based on a hierarchical Bayesian model, has been applied in recent years; Asada 2014).

This monitoring data of local deer density enables a chrono-sequence analysis of vegetation change concerning the increase in deer density or herbivory pressure. This is the greatest advantage of the Boso Peninsula as a study site. We first chose approximately 70 sampling sites at which we surveyed ground vegetation. In summer 2005, we set five 2 m × 2 m quadrats at each sampling site, and for each quadrat we noted every plant species present and estimated the cover (0–100%, visual counting) of each species. We also estimated the total foliar cover of the ground vegetation in each quadrat. For the period of 1996–2004, we estimated the deer density index by calculating the mean fecal pellet count (per square meter;

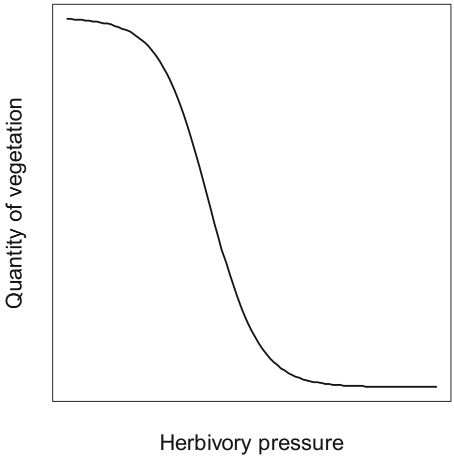

Fig. 24.1 An ideal S-shaped relationship between vegetation quantity and herbivory pressure

the sum of pellets/the number of monitoring years) for each sampling site (Suzuki et al. 2008).

A biplot can be drawn from the above data for the mean foliar cover of five quadrats and the deer density index. The assumption was that this biplot could be regarded as a chrono-sequential expression of the vegetation change as related to the increased herbivory pressure.

Before obtaining the data, we expected an S-shaped plot, similar to that in Fig. 24.1, between vegetation quantity and herbivory pressure. The S-shaped pattern would mean that the ecosystem shows little change when herbivory pressure is low, but significant degradation occurs after a threshold value of herbivory pressure is exceeded (Côté et al. 2004). This pattern is expected to be found in real data of herbivore density and vegetation mass if plants show resistance (e.g., exhibit anti-herbivore toxins or repellants) and/or resilience (e.g., complementary growth and recovery from the damage) when herbivory pressure is low, but such resistance/resilience ceases to be effective against intensive herbivory. This model seemed promising, because sika deer and plants in the Boso Peninsula have coexisted from prehistorical times to very recently—only 100 years ago, when sika deer were nearly extirpated—and thus the plants were likely to possess resistance/resilience against damage caused by deer. The actual biplot of vegetation cover and deer density index was compared with the hypothetical pattern in Fig. 24.1.

The plot of the actual data was completely different from the expectation; the vegetation cover showed simple decreasing functions against the deer density index (Fig. 24.2). Ground vegetation of the Boso forests simply decreased as deer population density increased, without showing any sign of threshold change. This fact indicates that there was no sign of tolerance or resilience of forest vegetation against deer herbivory. The significant decrease of vegetation cover at relatively low levels of deer density was probably caused by the rapid decrease of dominant species, such as *Arachniodes standishii* and *Aucuba japonica*, both of which are superabundant in the absence of deer but vulnerable to herbivory damage. These species, which are

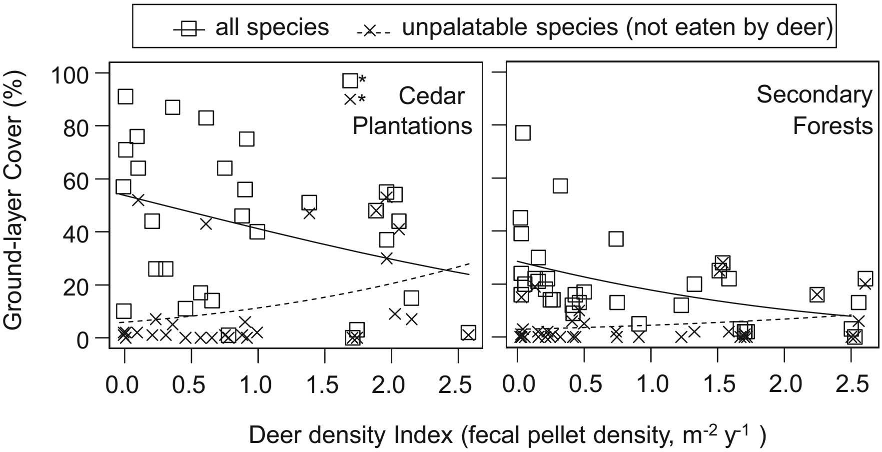

Fig. 24.2 Actual relationships between ground-layer vegetation cover and the density index of sika deer in the Boso Peninsula in 2005. Reproduced from Suzuki et al. (2008) with permission from the publisher

very common across the warm-temperate region of Japan, have large biomass and thus are highly competitive. However, these species do not have defensive traits, such as thorns, prickles, toxins, and repellants, and are thus favored by sika deer. These species did not survive, even at low deer density, and their disappearance resulted in a rapid decrease of the total ground vegetation. This lack of herbivory tolerance in dominant plant species is curious, considering that sika deer were common in the Boso Peninsula until roughly 100 years ago. The reason for this intolerance to herbivory may be attributable to the history of forests in the Boso Peninsula, which we will discuss in the next chapter (see Chap. 25).

Another biplot of species richness (the mean number of plant species that appeared in each sampling site) and the deer density index showed a unimodal, hump-shaped pattern (Fig. 24.3) that was expected by the dynamic equilibrium theory (Huston 1979) or the intermediate disturbance hypothesis (Connell 1978). In sampling sites where sika deer have recently invaded, the cover of *A. standishii* and *A. japonica*, competitive and herbivory-intolerant species, was slightly lower than in sampling sites where deer were absent. Instead, these sites included many common and less-competitive species, which increased the species richness of the site. At sites of high deer density, almost no plants were observed, except for a few species of high herbivory tolerance. If this pattern represents the chronological change after the invasion of sika deer, the species richness of plants seems to increase immediately after deer invaded but later gradually decreased with increased deer population.

Interestingly, the species composition showed clear turnover across the gradient of herbivory pressure, from competitive species to herbivory-tolerant ones (Suzuki et al. 2013; Fig. 24.4). This gradient suggests biological filtering by plant-plant competition and herbivory pressure that sorts plant species in opposite directions at

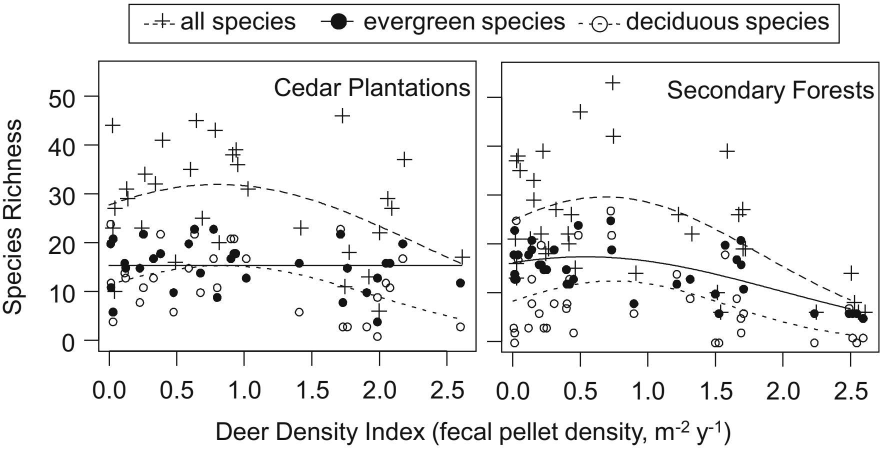

Fig. 24.3 Relationships between the species richness of ground-layer vegetation and the density index of sika deer in the Boso Peninsula in 2005. Reproduced and modified from Suzuki et al. (2008) with permission from the publisher

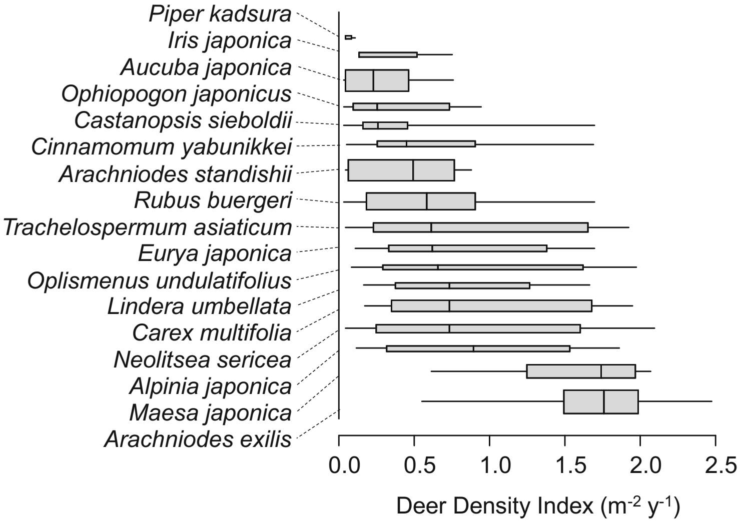

Fig. 24.4 Turnover of major plant species with the change in deer density index (DDI). A set of box, vertical bar, and horizontal bar represents 5, 25, 50, 75, and 95% of the DDI values of the study sites where the species appeared

low and high deer densities. Species richness of plants was maximized at intermediate levels of deer density index, at which both competition and herbivory were only weakly apparent. The maximization of species richness occurred at relatively low levels of deer density, possibly because the environmental productivity was low at the dark forest floor.

Another finding from this study was that the response of ground vegetation to deer density was different between conifer plantations and secondary forests. Comparing areas at the same level of deer density, conifer plantations tended to keep denser foliar cover than did secondary forests (Fig. 24.2). This difference is not attributable to habitat utilization of deer—as evidenced by camera trapping and GPS tracking, deer in the Boso Peninsula do not show any preference for either forest type. The difference in response between forest types was reported by Yanagi et al. (2008), in a leaf-cutting experiment mimicking deer herbivory. The authors found that soil conditions (bulk density and porosity) of cedar plantations were less sensitive to the treatment compared to soil conditions in natural broad-leaved forests. Yanagi et al. (2008) proposed that this result might be attributable to the character of cedar leaves, which hardly decompose and pile up densely on the topsoil, protecting it from physical damage. If the dense litter of cedar leaves buffers the topsoil against deer impacts, it may also reduce or mitigate negative feedback from the soil to the aboveground vegetation. Cedar plantations in Japan are generally considered to have little conservational value, but they may support the survival of plants under high deer density. Additionally, the canopy openness and the topography-derived moisture tend to increase the cover of ground vegetation (Suzuki et al. 2008). The result is also compatible with Akashi's (2009) model that predicted the resilience of understory vegetation to deer browsing based on both deer density and canopy gaps. Thus, appropriate thinning and slashing may increase canopy openness and enhance the resilience of vegetation against deer damage, as well as increase species diversity of many taxa (e.g., Ito et al. 2003; Taki et al. 2013). In addition, if the broad-leaved forests are more susceptive to deer impact than are cedar plantations, a higher conservational priority may be needed to protect the natural vegetation of forests.

In summary, the response of the forest ground-layer vegetation to sika deer in the Boso Peninsula was as follows. (1) Vegetation simply decreases as deer density increases. (2) Competitive species, which dominate the ground-layer in the absence of deer, are gradually replaced by herbivory-tolerant species as the sika deer population increases. At a relatively low density of sika deer, both types of plants can exist, and at this point, the species richness is maximized. (3) Abandoned secondary forests have a lesser amount of vegetation than do cedar plantations at the same deer density, suggesting the lower tolerance of such forests against herbivory. It should be noted, however, that the above patterns are interpreted from data collected from many points in time; these data points serve as "snapshots" of long-term change. Actual time-series changes can be detected only by tracking the long-term change of vegetation, as we show in the next section.

24.3 Legacy Effects of Deer Impact

In the summer of 2016, 11 years after the above survey, we revisited the sampling sites to monitor the change in vegetation and investigated the litter layer and physical properties of the topsoil (Harada et al. 2020). The density distribution of the sika deer

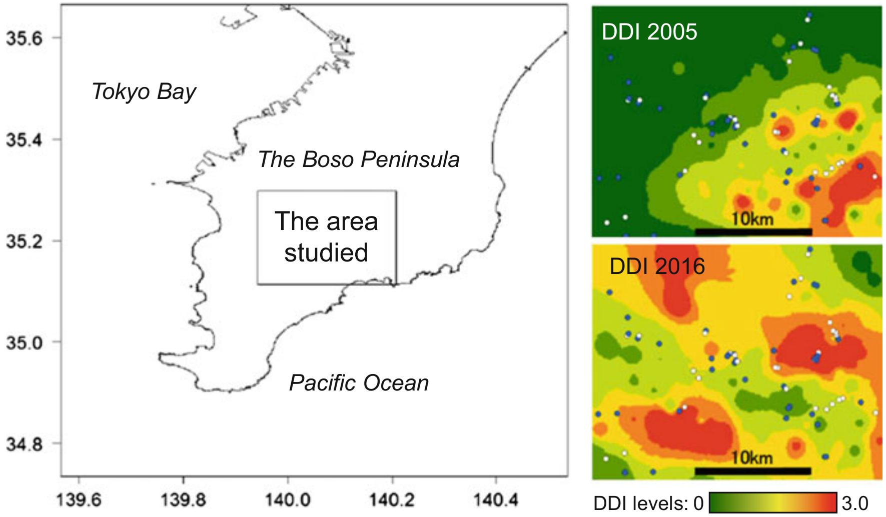

Fig. 24.5 The change in deer density distribution from 2005 to 2016 (*right*) across the range of study sites for the vegetation survey (*left*). Locations of the study sites are indicated with blue (conifer plantations) and white (secondary forests) circles in the graph on the right. Reproduced from Harada et al. (2020) with permission from the publisher

population had changed during the 11 years, with the population decreasing in the core region and increasing in the marginal region (Fig. 24.5). The objective of this follow-up study was to reveal the vegetation changes with respect to 11 years of herbivory pressure. We were especially interested in the 15 regions where deer density was reduced until 2016, expecting that the vegetation may have recovered in those regions. The deer density index, based on the data of the most recent nine years, was calculated for comparison with the previous study. We then determined whether there was a relationship between the vegetation cover and the new deer density index at each sampling site.

The biplot of the vegetation cover and the deer density index in 2016 revealed a different pattern from that in 2005 (Fig. 24.6). The two regression curves in Fig. 24.6 must have overlapped if the impacts of deer are reset in every short period. In conifer plantations, however, the regression curve for 2016 data was significantly lower than that for the 2005 data. This suggests that the vegetation in 2016 carried the legacy of deer impact that occurred more than 9 years before. A decadal legacy of deer impact may sound surprising, but it is fairly probable, considering that other researchers have found a legacy of deer impacts that last decades later (Nuttle et al. 2014; Tanentzap et al. 2009; White 2012). Such a change in regression curves was not observed in the secondary forests in our study, but this seems to be because vegetation had been almost completely removed before 2005, and thus no further degradation was possible.

To consider the reason why the influence of deer was not reset but carried forward in the system, the change in vegetation cover between 2005 and 2016 was analyzed

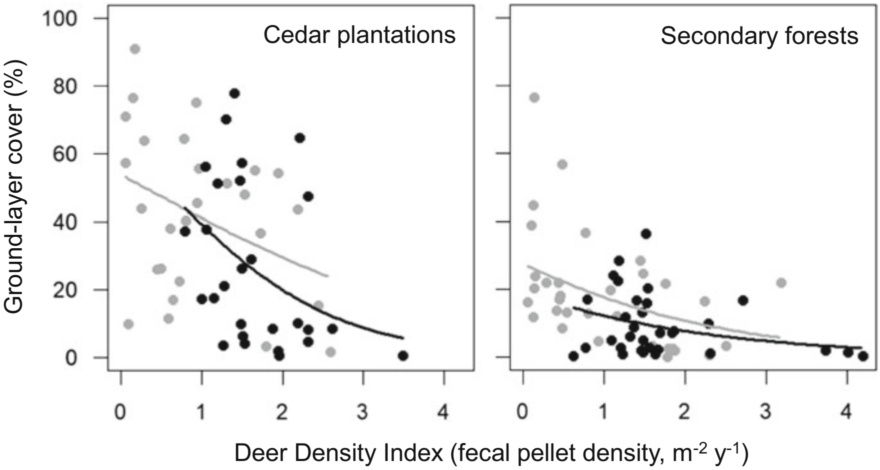

Fig. 24.6 Ground-layer vegetation cover measured in 2005 (gray) and 2016 (black) co-plotted with DDI calculated for the study site. Reproduced from Harada et al. (2020), with permission from the publisher

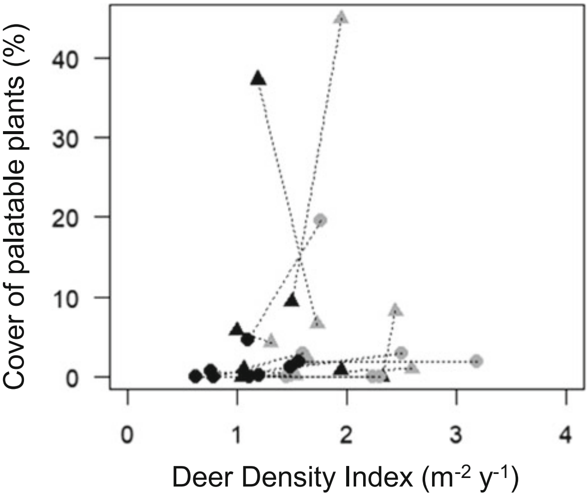

Fig. 24.7 Changes from 2005 (grey) to 2016 (black) in foliar cover of plants palatable to deer. Only plotted are the sites where deer density index decreased from 2005 to 2016. Reproduced from Harada et al. (2020), with permission from the publisher

separately for plant groups that are palatable to deer and those that are unpalatable. Palatable groups did not increase at 10 out of 15 sampling sites where the deer density index decreased (Fig. 24.7). At these sampling sites, seed sources might have been depleted after such a long absence of mother plants. Plants of unpalatable groups were still retained in many forests, but they did not show a remarkable increase. This result was incompatible with the well-reported trend that herbivory pressure promotes the establishment of recalcitrant ground vegetation, composed of plant species unpalatable to deer (e.g., Horsley et al. 2003; Stromayer and Warren 1997). Once such a recalcitrant layer is established, it can become overabundant and inhibit the recruitment of tree species (Royo and Carson 2006). This phenomenon did not take place in our study, possibly because the low light level at the forest floor limited the growth of unpalatable plants. As discussed in the next chapter, most unpalatable species in the Boso Peninsula can survive high herbivory pressure, but they seem to require sunny conditions (open canopy) to achieve a high growth rate. For this reason, unpalatable plants in closed-canopy forests are unlikely to serve as a buffer for forest systems facing high herbivory pressure. In another study on Yakushima Island, it was reported that seedling mortality had decreased for both unpalatable trees and palatable ones (Tsujino and Yumoto 2004), although this was attributed to the decrease in the physical effects of deer (see Chap. 19).

A legacy of deer overabundance was detected in belowground as well as aboveground vegetation. Our analyses, using structural equation modeling (SEM), suggest that the reduction of ground-layer vegetation in cedar plantations further reduced litter depth and, consequently, made the topsoil more compact (Fig. 24.8). Considering that in the experiment by Yanagi et al. (2008), no impact path from vegetation to litter layer and soil physical conditions was found, such indirect paths may need more time to accumulate and be detectable. Soil compaction is caused by repeated

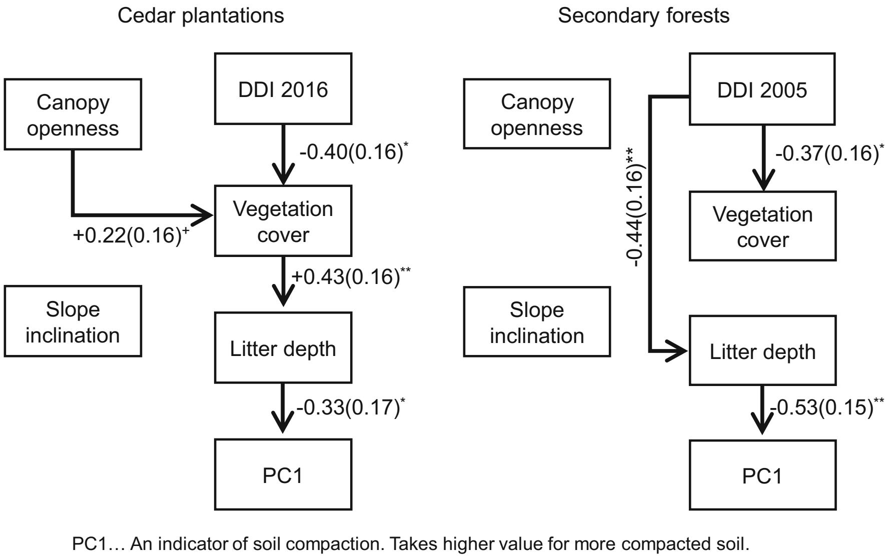

Fig. 24.8 The direct and indirect effect paths from DDI to the depth of the litter layer and the physical condition of the topsoil (best estimation model of the structure equation modeling or SEM). DDI2016 and DDI2005: DDI in 2016 and 2005, respectively. Reproduced from Harada et al. (2020), with permission from the publisher

physical impacts, such as trampling and rainfall on bare soil; thus, this compaction process requires a lengthier period. Soil compaction was also observed in secondary forests, but the effect path was different from that in the cedar plantations. In secondary forests, the deer population of 11 years ago—rather than that of recent years—had reduced the litter depth, resulting in soil compaction. This result was compatible with the experiment results by Yanagi et al. (2008), which suggested a higher likelihood of topsoil compaction in secondary forests than in cedar plantations. As they suggested, the topsoil in secondary forests may be more easily impacted by deer and might have already been compacted by deer 11 years earlier.

The more important question is whether the soil compaction due to deer impact inhibits the recovery of ground vegetation. We attempted to include feedback paths from topsoil to vegetation in the SEM, but this did not improve the goodness-of-fit and the explanatory power of the models. Whether this result was due to the shortage of replication or true absence of feedback path from topsoil to vegetation, we cannot say with certainty. In general, feedback paths have rarely been observed in forest-deer systems; even in the study by Wardle et al. (2001), an exhaustive study that revealed the influence of at least 13 years of deer exclusion on the above- and belowground conditions, significant feedback was not detected from the below- to aboveground conditions. The difficulty of finding feedback paths in forest-deer systems may be partly because forest soil is primarily affected by canopy trees, which determine the microclimatic condition and the quantity and the quality of litter layer, whereas the effects of ground vegetation is limited. Nevertheless, other feedback paths than we surveyed here might have been present. For example, the loss of ground vegetation due to sika deer is reported to cause the loss of nitrate in a watershed (Fukushima et al. 2013). Another possible explanation is the negative response of mycorrhizal fungi to deer impact, and this negative response may reduce the growth of mutualistic trees (Kardol et al. 2014). These changes might only be detectable over longer time periods, compared with the changes seen in litter removal and soil compaction. If so, feedback degradation of above- and belowground components might be detected in the future in the Boso Peninsula forests.

24.4 Concluding Remarks

The impact of sika deer on the ground vegetation and soil condition in warm-temperate forests appears to be primarily affected by the canopy trees on which the microenvironment of the forest depends. This contribution of upper vegetation is the key difference between the forest-deer system and the grassland-livestock system. The increase in species richness seen in grasslands can also be seen in the plant communities of the forest floor when herbivory pressure is low and the environmental conditions are fairly productive (e.g., sunny and moist). Soil conditions in that situation will be tolerable for the system. However, under high herbivory pressure and low productivity, the biomass, species richness, and percent cover of plants decrease. In extreme cases, the ground-layer vegetation disappear almost completely, causing further degradation in the belowground system such as soil compaction. Such effects accumulate year by year and possibly inhibit the natural regeneration of plant communities even after the deer density is reduced. The enormous impact of sika deer we observed is partly attributable to the feeding behavior of sika deer as a browser-grazer; however, the extremely dark forest floor resulted from the socioeconomic changes in this region is another suspected reason of the vulnerability of this forest system to sika deer.

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Chapter 25
Successional Pathways of a Warm-Temperate Forest after Disturbance: Effects of Clear-Cutting and Herbivory

Maki Suzuki

Abstract There are major challenges in restoring forest vegetation that has accumulated damage by deer, and it is unlikely that such vegetation will recover on its own. In this chapter, we detail an experiment to recover forest vegetation that had been severely affected by cumulative damage from sika deer (*Cervus nippon*). The experimental site consisted of clear-cut plots, simulating canopy gaps, and control plots, which were closed canopy. One half of both the treatment (gap) plots and uncut plots were enclosed by fencing to exclude deer, leaving the other half of the plots under the effect of deer. Over the next 10 years, the fenced closed-canopy plots did not show remarkable recovery; in contrast, the gap plots came to be covered by rapidly growing, light-demanding plants, even with the presence of deer in the unfenced plots. The gap-and-fence plots gradually recovered forest vegetation. However, each of the gap-and-no-fence plots came to be covered by different plants that were unpalatable to deer. Based on these results, effective restoration strategies and future management protocols are discussed.

25.1 Introduction: Resilience of Forests to Deer Impact—The Aim of the Experiment

As we saw in Chap. 24, impacts of overabundant sika deer (*Cervus nippon*) tend to accumulate as a long-lasting legacy that often prevents recovery of vegetation and soil condition even after the density of the deer population has decreased. The legacy effects of deer overabundance are especially remarkable in low-productive environments, such as the forest floor in warm-temperate regions. In this chapter, we discuss how to restore natural forests that have been degraded by overabundant sika deer.

Before we discuss forest restoration, however, we need to reconsider the restoration target. Forest ecosystems are not static; under their inherent disturbance

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M. Suzuki (✉)
Department of Natural Environmental Studies, Graduate School of Frontier Sciences, The University of Tokyo, Kashiwa, Japan
e-mail: suzukima@edu.k.u-tokyo.ac.jp

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regimes, forests are frequently disturbed and naturally recover (Attiwill 1994). For such dynamic systems, conditions cannot be judged as “degraded” or “recovered” based on a temporary observation of relatively short term (Ghazoul et al. 2015). This dynamic feature is also shared by Japanese forests with sika deer populations. As we have seen in Chap. 24, forests and deer populations in Japan have both experienced drastic changes during the past century, following changes in socioeconomic structure. In the early to middle part of the last century, sika deer populations in Japan had decreased to near extinction due to culling and habitat losses. At the same time, woodlands in rural villages, in which sika deer had commonly been found, were abandoned after the fuel revolution in the 1950s–1970s (Oono et al. 2020) and gradually developed into mature forests. In these abandoned and maturing forests, the population of sika deer rapidly increased in the last 40 years, causing significant ecological impacts. Therefore, the rich vegetative cover that had been observed before the deer became overabundant was not a permanent state, but rather a temporary stage in the long-term forest dynamics. Considering such a background, simple recovery to the condition before deer overabundance would seem to lose its legitimacy as a conservation target. It is also true, however, that the current situation of ground vegetation and soil properties of these forests is far from ideal. Where then should we set the conservation goal if we want to improve the current situation?

My personal suggestion is to aim, even with the presence of sika deer, at letting the target forest sustain or recover its resilience or, at least, the potential to naturally return to its inherent state after every disturbance. Generally, a forest destroyed by natural or artificial disturbances tends to recover after a certain amount of time. The newly grown forest may not have the same species composition as that of the pre-disturbance system, but its ecological function can be similar to the previous one. It is thought that such a capacity for resilience is high with respect to a disturbance that repeatedly occurs in the forest (Kulakowski et al. 2017). In the case of Japanese forests, climatic hazards, such as typhoons and heavy snow, and repeated fuelwood gathering by rural residents can function as the inherent disturbance regimes of a regional forest (Hiura 1995; Iida and Nakashizuka 1995). These disturbance regimes, whether they are natural or artificial, are not simple destruction, but key elements that drive regeneration and maintenance of the forest (Attiwill 1994).

Additionally, repeated herbivory by native deer can also function as a non-destructive disturbance regime if the forest is resilient enough. Light but frequent damage caused by native herbivores, in combination with rare but intensive disturbances (whether natural or non-natural), affect the development and maintenance of the forest systems. From this perspective, both the system-inherent disturbance regime and the corresponding resilience are the goals of forest conservation (Kulakowski et al. 2017). Such target setting is not new and is becoming a global trend in forest management, especially in Europe and North America (Ghazoul et al. 2015). In this chapter, we apply this approach to the particular situation of sika deer in wooded landscapes in Japan. The aim is to maintain or recover forest resilience or the vegetation dynamics that always move toward a forest vegetation within the disturbance regime.

In light of this goal, the current state of the secondary forests of the Boso Peninsula may not necessarily be complete degradation. Lost ground vegetation and compacted soil indicate that these secondary forests have already lost their resilience (i.e., they could not naturally revert to forests). This is not necessarily true, however, considering the historical disturbance regime. Until roughly half a century ago, these forests were coppice woodlands where the gathering of fuelwood and natural recovery formed an ongoing cycle (Okada 1999). The earliest stage of succession has been driven by fast-growing, light-demanding plants. These early-seral species are currently not observed in the ground-layer of late-seral forests, but their seeds remain buried underground and are potential seed banks (e.g., Hirayama et al. 2019). Many of these buried seeds can germinate in the right conditions, i.e., with drastic changes in soil temperature after canopy gap creation. Currently, the late-seral species that have gradually replaced early-seral species dominate the canopy layer of the present matured forests. Seedlings of these late-seral species (in the case of Boso, evergreen species of *Castanopsis* and *Quercus*) have been lost to herbivory at the ground level, but their seed rain is still available. In addition, dormant buds in oak trunks still retain sprouting activity, which increases once the major trunk is lost. As such, both early- and late-seral plants remain below- and aboveground levels of the forests impacted by sika deer and serve as the potential drivers of secondary succession after intensive disturbances (e.g., wind damage and clear-cutting). If these forests can remain resilient against large-scale disturbance, restoration efforts may not be needed.

Even so, it is still unclear whether the forests in the target region have truly retained their resilience, given that ungulate herbivores, including sika deer, can intervene in the successional pathway after intensive disturbance. Ungulate herbivores are reported to have various effects on the successional path, by selective herbivory on plant species (Prach and Walker 2020) and by indirect effects through soil conditions (e.g., Davidson 1993; Jefferies et al. 1994). One remarkable example is seen in the Allegheny Plateau in North America (Stromayer and Warren 1997). In this region, white-tailed deer reduced tree seedlings in the understory of pre-cutting forests while leaving plants that were resistant or resilient to herbivory undamaged. Subsequent removal of canopy trees further boosted the increase of these plants and ultimately created a dense weed layer. According to a long-term experiment in Allegheny, the higher the deer density were during the first decade after a cutting event, the denser the weed layer grew and prevented the establishment of hardwood trees (Horsley et al. 2003). A follow-up study of this experiment revealed that the “recalcitrant” understory vegetation (Royo and Carson 2006) created by the deer prevented the recovery of forest vegetation for up to two decades after the deer were removed (Nuttle et al. 2014). This case is among several examples of deer affecting succession through intervening in the competition between trees and non-tree plants. Additionally, degradation of the belowground system, such as soil compaction (Chap. 23), may also prevent the recovery of forests. To judge whether a forest affected by ungulate herbivores is still resilient against a disturbance, we need long-term tracking of vegetation dynamics after the disturbance.

For this reason, our laboratory, in cooperation with the University of Tokyo Chiba Forest (UTCBF), launched a field experiment to track the vegetation dynamics for more than a decade after clear-cutting. This experiment was designed to give insights to the following questions: (1) Is the poor recovery of ground vegetation solely attributable to high herbivory pressure? Or, is the low level of light at the forest floor also involved? (2) Does herbivory on seedlings and saplings before a disturbance event (clear-cutting) cause permanent regeneration failure? Or, can regeneration be driven by soil seed banks, seed dispersion, and sprouts from cut stumps? (3) If the high herbivory pressure by deer continued after the disturbance (clear-cutting), does it manipulate succession trajectory and prevent forest recovery? In the following sections, I explain the experimental setting and the results of the first decade. On the basis of these results, I discuss the possible measures to maintain forest resilience with the presence of deer populations.

25.2 Experimental Setting

The experimental system was set in the UTCBF, located in the core distributional area of sika deer in the Boso Peninsula. Mean annual temperature of this region is approximately 13.2 °C, and mean annual precipitation is approximately 2200 mm. Experimental plots were set in three stands of abandoned coppice woodlands, which were each 2–5 km apart (35.8–11° N, 140.7–9° E; Fig. 25.1). Clear-cutting for fuelwood harvesting ceased in the 1950s, and, afterward, these areas were abandoned. Originally, the canopy layer of these areas was occupied by a variety of evergreen species, including *Quercus glauca* and *Quercus acuta*, *Castanopsis sieboldii*, *Ilex integra*, and *Machilus thunbergii*, which were accompanied by species of subcanopy trees (e.g., *Eurya japonica*, *Dendropanax trifidus*, *Cleyera japonica*, *Myrsine seguinii*, and *Camellia japonica*). Several plant species including evergreen

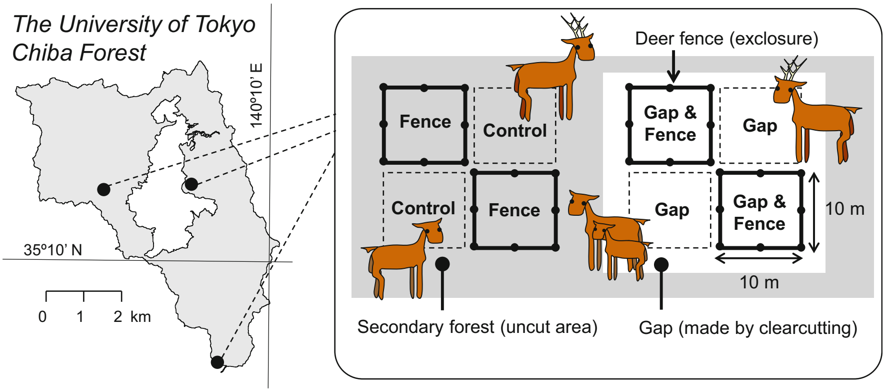

Fig. 25.1 The experimental plots

shrubs (*Maesa japonica* and *Damnacanthus indicus*), lianas (e.g., *Anodendron affine*), and ferns (*Arachniodes sporadosora*) showed sparse distribution on the dark forest floor before the experimental treatments. Deer density during 1986–2006 were estimated by the UTCBF as 2–13, 4–24, and 2–15 deer per km^2 for each of the three stands (Yamanaka 2007).

Each experimental stand was composed of eight 10 m × 10 m plots (Fig. 25.1). From February to March 2008, the University Forest staff cut all trees within a 20 m × 20 m area in each stand, to totally remove vegetation from four of the eight experimental plots. The staff did not intend to remove ground vegetation, but because ground vegetation had already been removed by sika deer, the cutting activity created mostly bare land. Coarse woody debris created by the cutting was removed. Immediately after clear-cutting, two plots under a closed canopy and two plots under gaps were enclosed by 1.5-m high fences that excluded sika deer. In total, one experimental plot included four treatments (clear-cutting or no cutting; deer exclusion or no exclusion) with two replications each.

The monitoring of vegetation began in 2007, 1 year before the experiment started. Ground vegetation was monitored in 2007, 2008, 2009, 2012, and 2015, using five 1 m × 1 m quadrats for each 10 m × 10 m plot. The monitoring is continuing but with larger quadrats (5 m × 5 m) to follow the grown vegetation. Here I report the results during 2007–2015. The physical conditions of the topsoil were checked in 2011, using 400-mL soil cores taken at the centers of the 10 m × 10 m plots. Details of these results are available in published articles (Suzuki 2013; Suzuki and Ito 2014; Suzuki et al. 2021).

Comparison of the ground vegetation between the fenced and unfenced plots under closed canopy was expected to reveal whether the limited recovery of vegetation was purely attributable to current deer population density. No recovery in the fenced plots under closed canopy would indicate legacy effects that cannot be mitigated solely by removing deer. Additionally, comparison of the vegetation dynamics between plots with and without clear-cutting would indicate whether the legacy effect causes a permanent regeneration failure after a disturbance event. Finally, comparison between the fenced and unfenced plots after clear-cutting was expected to reveal how post-disturbance herbivory manipulates succession trajectory and how it affects forest recovery.

25.3 Early-Stage Vegetation Dynamics after Disturbance

Differences in the vegetation status among the treatments were already apparent after 1.5 years from the start of the experiment (Fig. 25.2). Almost no vegetation was found under closed canopy in the fenced plots or in the unfenced plots. This suggests the legacy effects of deer as commonly observed in dark forest floors of matured forests. In contrast, vegetation cover in plots that were clear-cut exceeded 10% only half a year later, irrespective of the presence of deer. Up to the monitoring date in 2009 (1.5 years from the clear-cutting), the vegetation cover in the gap plots reached

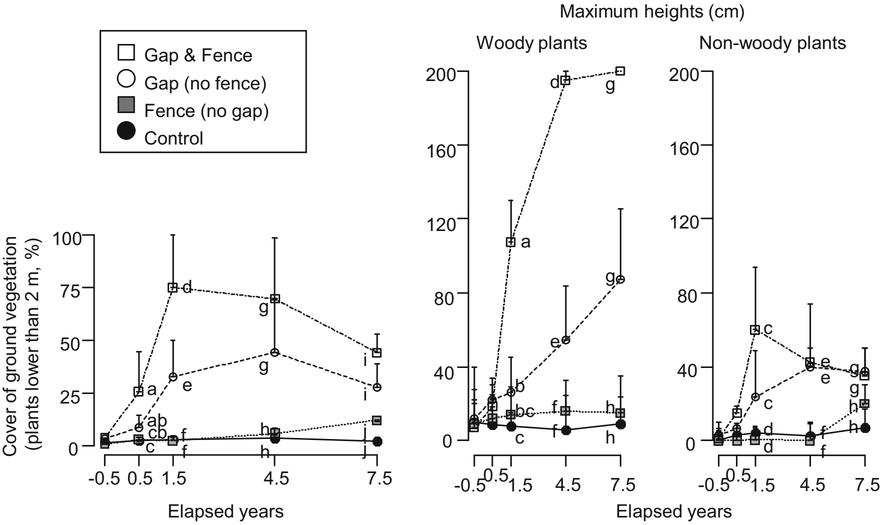

Fig. 25.2 The change in vegetation cover and plant height. Experimental treatments (clear-cutting and exclosure installments) were carried out in spring 2008. Data were taken in the summer of 2007, 2008, 2009, 2012, and 2015 (−0.5, 0.5, 1.5, 4.5, and 7.5 years after the experiment started). For each census year, pairs of significantly different values are marked with different letters. Reproduced from Suzuki et al. (2021) with permission from the publisher

75% inside the fenced plots and 30% in the unfenced plots. Despite the legacy effect, the ground-layer vegetation rapidly increased after gap creation; therefore, the accumulation of deer impact before the disturbance (clear-cutting) did not result in a permanent failure of vegetation recovery.

This rapid recovery was led by the germination of seedlings from the buried seeds. The species we observed in summer 2008 included grasses (e.g., *Miscanthus sinensis*), herbs in the Asteraceae family, and exotic fireweeds (*Erechtites hieracifolia* and *Crassocephalum crepidioides*); seedlings of deciduous trees known as early-seral trees (e.g., *Zanthoxylum ailanthoides*, *Mallotus japonicus*, and *Rhus javanica* var. *chinensis*) were abundant inside the fenced plots but were rare or absent in unfenced plots, in which it can be assumed that deer browsed the understory (Fig. 25.3). Because these species were not observed around the experimental plots before clear-cutting, their germination from the soil seed bank is the most probable explanation. These plants are very common in large forest gaps created by felling in the southern part of Japan. These early-seral species require strong light and thus have evolved the capacity for long-lived seed banks belowground, which can persist through dark phases between cutting events (Hirayama et al. 2019). It is not surprising that the seeds of early-seral species were still viable (even after the cutting event of 50–60 years ago) and successfully germinated in the experimental plots. It is possible that the rapid environmental change induced germination and the vegetation dynamics of early-successional stages. In this way,

Fig. 25.3 The first stage (0.5 years from the clear-cutting) of the vegetation dynamics in a gap plot without the deer fence. Fireweeds (*Erechtites hieracifolia* and *Crassocephalum crepidioides*) and unpalatable plants (not eaten by deer) were abundant at this stage. Although bushy shoots sprouted from the cut stumps of trees, most of these shoots were consumed by deer within a few years

the response of the seed bank to disturbance can be regarded as the resilience factor that ensures rapid recovery of vegetation immediately after a cutting event.

Interestingly, exotic fireweeds (*E. hieracifolia* and *C. crepidioides*) suddenly appeared in the newly created gaps, even though they had not been observed in the plots before clear-cutting. These plants were introduced from North America, where they are known to form a large patch right after intensive disturbances such as forest fires or clear-cuttings. Additionally, these plants are usually not eaten by sika deer (Takatsuki 1984). Probably for these reasons, fireweeds grew rapidly immediately after clear-cutting both within the fenced plots and in the unfenced plots. There was some concern that these unpalatable species might spread further and affect succession. However, the fireweeds mostly disappeared from all plots before the monitoring date in 2012 (4.5 years from the clear-cutting), giving no continuing impacts on the vegetation dynamics. These plants might be adapted to full-sun conditions that temporarily appear after severe disturbance and thus are not effective in changing the direction of vegetation dynamics.

25.4 Effects of Herbivory on the Vegetation Dynamics

The vegetation in the gap-and-fence plots developed following a typical trajectory commonly observed in the studied region (Figs. 25.2 and 25.4). A group of rapid-growing and light-demanding plants such as graminoids (e.g., *Calex* spp. and *M. sinensis*), deciduous trees (e.g., *Z. ailanthoides* and *M. japonicus*), and shrubs (e.g., *Deutzia crenata* and *Callicarpa japonica*) were the first that germinated, possibly from dormant seeds, soon after the clear-cutting; slightly later, other light-demanding deciduous species (e.g., *Cerasus jamasakura* and *Stachyurus praecox*) also germinated, and the seedlings grew. Species richness of the ground-layer in the gap-and-fence plots peaked in summer 2009 (1.5 years after the treatment) and then began to decrease until summer 2012, reflecting the immigration stage and later species sorting due to interspecies interaction. This is exactly the pattern of succession commonly observed after clear-cutting in the warm-temperate region of Japan, where forests are not affected by the pre-disturbance damages caused by sika deer. This result suggests that the pre-disturbance impact by deer did not change the succession trajectory. However, continued impact by deer after the disturbance could change the succession trajectory, whereas the trajectory is unaffected if the deer were excluded immediately after the disturbance.

The vegetation dynamics in the gap-and-no-fence plots were quite different from the above trend. Until summer 2015 (7.5 years after the clear-cutting), these plots came to be occupied by unpalatable plants or plants that exhibited anti-herbivory defenses such as toxins or repellent (e.g., *I. anisatum*, *M. japonica*, and *N. sericea*) or thorny organs (e.g., *Osmanthus heterophyllus*, *Rubus microphyllus*, *Rosa luciae*, and

Fig. 25.4 Vegetation dynamics in a plot with the gap-and-fence treatment. Left: germination (probably from seed banks) and sprouting from cut stumps where the plants first established after the clear-cutting. Middle: vegetation after 3.5 years from the start of the treatment. Canopy layer (2–3 m in height) was dominated by a species of pinnately compound leaves, *Zanthoxylum ailanthoides*, which is a typical fast-growing and light-demanding species. Right: height of canopy trees exceeded 5 m at the time this photograph was taken. Shade-tolerant evergreen trees are growing and have almost reached the height of canopy trees

Fig. 25.5 Different species compositions observed in four 10 m x 10 m plots of the gap-and-no-fence treatment. Clockwise from top left: shrubland of *Maesa japonica* with saplings of unpalatable trees (*Neolitsea sericea* and *Pinus densiflora*); saplings of unpalatable trees (*Osmanthus heterophyllus* and *N. japonica*); a bush of a thorny shrub, *Rosa luciae*; and a grassland of *Miscanthus sinensis* accompanied by unpalatable shrubs (*M. japonica* and *Zanthoxylum piperitum*)

Zanthoxylum piperitum). These species showed limited growth and sparse distribution on the dark forest floor, but clear-cutting drastically changed this environment, and in sunny conditions these plants rapidly grew. Especially in the gap plots outside the fences, the unpalatable plants rapidly grew both in terms of cover and height. There was also an increase in graminoids and thorny shrubs that were resilient to deer herbivory or plants that grow faster than the consumption rate by deer (e.g., *M. sinensis*, *R. microphyllus*, *R. luciae*, and *Z. piperitum*). In addition, a few tree species that are unpalatable to deer (e.g., *I. anisatum*, *O. heterophyllus*, and *N. sericea*) showed intensive recruitment, presumably from dispersed seeds, in the gap-and-no-fence plots. The foliar cover—consisting of mainly unpalatable plants—reached almost 100% in the gap-and-no-fence plots, until the monitoring date in 2015 (7.5 years after the clear-cutting). Note that each 10 m x 10 m plot was occupied by different plant species (Fig. 25.5). One plot contained the toxic tree *I. anisatum* and the thorny shrub *R. luciae*; another one became a grassland containing mostly the tall grass *M. sinensis*, with a small mixture of *Z. piperitum*. Another plot became shrubland composed of thorny *O. heterophyllus* and *N. sericea*,

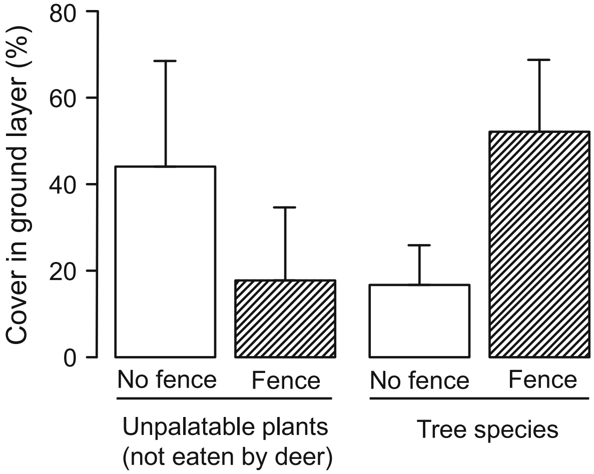

Fig. 25.6 Contrasting effects of fencing (deer exclusion) on trees and unpalatable plants in gap (clear-cutting) plots. Each bar graph represents the cover of each plant group in the ground-layer in 2015. Unpalatable plants were dominant where deer were present. Within the exclosures, these unpalatable species were less frequent, presumably due to the shade of the tree species. Reproduced from Suzuki et al. (2021) with permission from the publisher

as well as the dense shrub *M. japonica*. This variety in the type of vegetation is likely attributable to the priority effect; that is, the impact of the newly arrived species on the developmental process of the vegetation (Fukami and Futuyma 2015). As well, deer herbivory after the disturbance might have increased the spatial heterogeneity of the vegetation.

Interestingly, this group of unpalatable, native species have since disappeared from the gap-and-fence plots, where they were possibly outcompeted by species that are palatable to deer (Fig. 25.6). It appears that the presence of deer acts as an indirect support of unpalatable species; the deer eat the competitor plants, at least during the first several years, until the unpalatable plants then direct the vegetation dynamics (the importance of time for the early colonist to establish its population has often been suggested; e.g., Robinson and Edgemon 1988). A similar situation was seen in the Allegheny Plateau, where the deer population density after the cutting event determined the abundance of unpalatable plants. Both in the Allegheny and at our study site, the successional trajectory was changed only when herbivory pressure continued after the disturbance. This is a bit different from the pattern that is expected in the general model of the alternative successional trajectory (e.g., Suding et al. 2004), in which a modification to the system at the pre-disturbance stage decreases the system resilience and causes a drastic shift in the system dynamics. However, deer may modify the system at the post-disturbance stage and affect the vegetation dynamics after the cutting event.

An important question is whether the vegetation dynamics in the gap-and-no-fence plots are arrested at the mid-point of the normal trajectory or are already following an alternative successional trajectory (Horsley et al. 2003; Nuttle et al. 2014). If the current situation is an arrested succession (Gibson and Brown 1992) the unusual vegetation may be a temporal state; if the vegetation is on an alternative trajectory, however, the resilience of the forest is considered to have been lost. So far, these vegetation patterns look quite unlike the early-seral vegetation of the gap-and-fence plots, which means that we can reject the possibility that the gap-and-no-fence plots are on the same successional pathway as that of the plots inside fences. In addition, most tree species, except a few unpalatable ones, could not establish in the plots outside the deer fences. These facts suggests that the vegetation dynamics of the gap-and-no-fence plots are already on track to a non-forest vegetation pattern, rather than being simply arrested in the middle of the usual successional path. Such a hypothesis requires further examination; for example, continuous monitoring of vegetation dynamics after the deer population shrinks in the future.

25.5 Response of the Belowground Systems

According to the data in 2011 (3 years after the experiment started), the clear-cutting and fencing had opposite effects on the belowground system of the experimental plots (Suzuki and Ito 2014; Fig. 25.7). Both in the gap areas and under closed

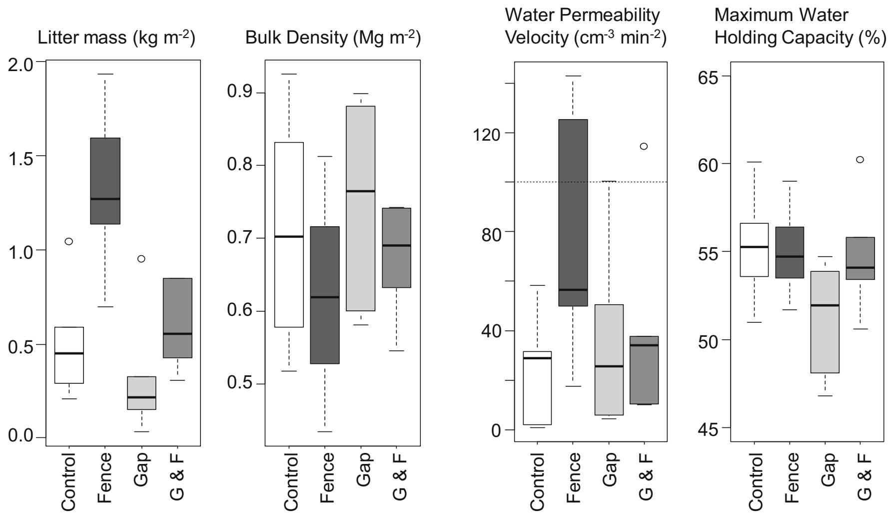

Fig. 25.7 Effects of the experimental treatments on the mass accumulation of the litter layer and physical conditions of the topsoil. Water permeability velocity and maximum water holding capacity are positively correlated with coarse and fine soil porosity, respectively. Reproduced from Suzuki and Ito (2014) with permission from the publisher

canopies, deer fences resulted in a thickening of the litter layer on the topsoil, relaxed soil compaction (i.e., decreased bulk density of topsoil with increasing soil porosity), and a corresponding increase in the rate of water permeability; however, the effects of fencing were not statistically significant. In contrast, gap creation significantly decreased litter mass on the top soil and significantly increased the fine porosity of the soil. Comparing the treatments, it can be seen that the effects of gap creation were relatively greater than those of fencing.

Soil compaction generally has a negative effect on plant growth, and thus the gap creation was expected to prevent the recovery of vegetation. As we have already seen, however, the soil compaction in the gap plots did not prevent establishment of new vegetation. Rather, in the gap-and-fence plots, the newly developed vegetation together with litter layer seemed to have protected the soil from the impact of rainfall and, consequently, mitigated the soil compaction. In contrast, the most pronounced degradation of soil properties was found in the gap plots without fencing. In this plot type, sika deer inhibited rapid recovery of tree species that otherwise could have sheltered the topsoil from the impact of rain and trampling. The result was further soil compaction and drying of the topsoil. As such, the post-disturbance impact by deer degrades soil properties as well as the aboveground vegetation. This degradation of soil properties may have further affected species composition; for example, by favoring xeric plants and plants that tolerate low levels of nutrients.

On the other hand, the treatment of fencing alone (closed canopies) resulted in less soil compaction, although recovery of ground-layer vegetation did not occur. The presence of fencing seemed to have a direct mitigating effect on soil compaction, for example, by preventing further trampling of deer or by stabilizing the litter layer that can protect the topsoil. These effects may indirectly support the decomposition activities of fungi and microbes (e.g., Wallace 1987; Rossow et al. 1997; Stark et al. 2003; Bressette et al. 2012).

At that time, the number of soil invertebrates collected from the litter layer by the hand-sorting method increased with the litter mass (Suzuki and Ito 2014). Because gap creation significantly decreased the litter mass, the gap-and-no-fence plots showed much lower density for most groups of soil fauna compared to what was found in other plots. Fencing of gap plots tended to mitigate this negative effect on the soil invertebrate community, although it cannot completely compensate for the decrease of invertebrates.

In total, the negative legacy of deer overabundance that caused soil compaction could be mitigated by simply installing a deer fence, which also triggered the positive response of soil invertebrates. This result does not coincide with the negative relationship between the deer density 11 years ago and current soil compaction (Chap. 24). This might be because the exclusion of deer (by fencing) has a stabilizing effect on the litter layer. Culling reduces deer population density but does not completely exclude deer from the surrounding area. On the other hand, a fence can completely exclude deer from the surrounding area, and such complete exclusion might effectively mitigate the negative legacy of deer herbivory. Whatever the mechanism was, however, mitigation of the soil compaction by fencing was not enough to trigger the recovery of the ground-layer vegetation, given that reduction in light levels is the primary limitation factor of regeneration of plants. Exclosure by fencing immediately after clear-cutting supported recovery of the aboveground vegetation and, consequently, prevented further degradation of the belowground systems. This may be an adequate option to trigger the automatic recovery of a forest from the accumulated impact of deer.

25.6 Concluding Remarks

The results of the above experiment suggest that the forest in our study site has retained the potential to move toward a fully vegetated forest. To drive the natural recovery of forest vegetation, however, the system needs temporary removal (by exclusion) of the deer population until the newly recruited saplings establish their competitive advantage. Otherwise, plant species that are unpalatable to deer tend to have the advantage and lead the vegetation to unusual, non-forest landscapes. As a side note, our study sites were hit by an extraordinary typhoon in late summer 2019, and the storm caused trees to fall and breach the fence that had guarded a gap-and-fence plot from herbivory. However, since that time, the vegetation in the plot is still growing with maintaining appearance of a typical young forest. This observation suggests that 10 years of fencing was long enough to reset the vegetation dynamics to a trend toward forest recovery.

Our experiment does not include a treatment to simulate a low population density of deer; thus, we cannot judge if the forest can recover after disturbance with the presence of a deer population at low density. However, because forests in this region have overcome repeated clear-cutting along with the continuous presence of sika deer, the forests are likely to recover at low deer density. Also in a study of the forests of the Allegheny Plateau, it was found that keeping a low deer density immediately after clear-cutting did not have enough of a “nursery” effect to support the establishment of unpalatable plants (Nuttle et al. 2014). Therefore, the forests in our study site might be able to recover after clear-cutting without fences, but only if the deer density is low. Further experiments are needed to test this hypothesis.

The lack of plant recruitment in the fenced plots under the closed canopy emphasizes the importance of traditional clear-cutting as a disturbance regime of the forests in this region. The light limitation in the current forest floor setting is the result of the cessation of cyclic fuelwood gathering. This is also the environment in which deer population increased and the consumption by deer overcame the productivity of the ground vegetation. This might be the reason why the ground-layer vegetation came to be so intolerant to herbivory, as we saw in the previous chapter. If so, the current degradation of vegetation and soil in the Boso Peninsula may not be solely attributable to deer overabundance; it might have also resulted from an unfortunate combination of deer population dynamics and forest dynamics.

If this is the case, forest conservation cannot be achieved solely by the control of the deer population; it is neither appropriate nor realistic. Native deer are a part of the forest ecosystem, and their complete removal cannot be a conservation target.

Instead, a combination of deer population control and forest vegetation dynamics can be, in some instances, an effective option. Resetting the vegetation dynamics by temporarily excluding deer may be the "kick-start" needed to recover a vegetation-rich forest.

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Chapter 26
Effect of Different Periods of Chronic Deer Herbivory on Both Tall Forbs and Soil Seed Banks Following Deer Exclusions in a Damp Beech Forest

Atsushi Tamura

Abstract This chapter focuses on evaluating the effects of chronic deer herbivory on recovery of tall forbs and composition of soil seed banks following exclusion of deer in a damp beech forest. I used deer exclosures of different ages, which are established in 1997 (E1997), 2003 (E2003), and outside (OUT). Densities of four forb species of 12 targeted species were significantly greater in E1997 than in E2003, and the ratio of mature ramets to all ramets of one species tended to be higher in E1997 than in E2003. These results suggest that the 6-year different periods of chronic deer herbivory before the exclosures were established caused delay of recovery in densities or decrease in densities in E2003. The seed bank study revealed that one individual of vulnerable species to deer grazing emerged only in E1997; in contrast, many invulnerable species emerged in E1997, E2003, and OUT. Relative dominance of invulnerable species was higher in E2003 than in E1997, and relative dominance of forest forb species was lower in E2003 than in E1997. These results indicate that the vulnerable forb species can seldom form soil seed banks, but invulnerable and forest forb species can form soil seed banks, and restoration of vulnerable forbs cannot rely only on seed germination from the soil seed bank despite chronic deer herbivory. To conserve vulnerable forest composed of the forb-dominated floor, conservation measures are needed during the period when the organs of the plant still remain in the aboveground.

26.1 Introduction

Increasing deer populations cause extensive damage to temperate forest ecosystems worldwide (Côté et al. 2004; Kirby 2001; Rooney 2001; Russell et al. 2001). In particular, forest forbs, the life cycles of which repeat within the range of deer height,

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A. Tamura (✉)
Division of Forest Research and Nature Restoration Planning, Kanagawa Prefecture Natural Environment Conservation Center, Atsugi, Japan
e-mail: tamura.a33@gmail.com

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are seriously susceptible to deer grazing (Rooney and Gross 2003; Webster et al. 2005; Whigham 2004). In Japan, sika deer (*Cervus nippon*) severely affect forest ecosystems (Takatsuki 2009), especially floor vegetation composed of tall forbs (Kato and Okuyama 2004; Ohashi et al. 2007; Tamura et al. 2005). At the species level, forest forbs, such as *Kirengeshoma palmata* and *Parasenecio farfarifolius* var. *acerinus*, are vulnerable to extinction due to sika deer herbivory (Ministry of the Environment, Japan 2015).

Conservation measures, such as establishing deer exclosures (hereafter, exclosures) or deer control, are used worldwide to restore vegetation; however, forest forbs might be difficult to recover following exclusion of deer herbivory; such species are *Trillium* spp. (Augustine and Frelich 1998) and *Lilium superbum* (Fletcher et al. 2001). Even with deer controls, recovery of forbs, e.g., palatable species, is limited compared to that of woody plants (Jenkins et al. 2014; Royo et al. 2010; Tanentzap et al. 2012).

Chronic deer herbivory could be one factor that made forbs difficult to recover, paired with their ecological characteristics. Whigham (2004) reported that almost no forest forbs produce new aboveground tissues in response to herbivory, suggesting that the timing and amount of herbivory would influence short- and long-term plant responses. This finding leads to the following process of forbs decline; i.e., forest forbs diminish in size, the density of flowering individuals decreases, seed sources deplete, and soil seed bank inputs decrease in proportion to chronic deer herbivory; as a result, the recovery of forb densities may be difficult even after conservation measures are conducted. Consequently, the species composition of floor vegetation may irreversibly shift towards an alternative stable state (Husheer et al. 2003; Kirby 2001; Ripple et al. 2010).

The Kanagawa Prefectural Government has established exclosures since 1997 to restore the floor vegetation composed of tall forbs in beech forests in the Tanzawa Mountains, eastern Japan. Additional exclosures were established in 2003 close to the 1997 exclosures. Thus, this area has favorable conditions to assess vegetation recovery through different periods of chronic deer herbivory.

This chapter aims to review the effect of periods of chronic deer herbivory on tall forbs and soil seed banks following deer exclusion in a damp beech forest through analyzing (1) density of forbs and (2) herb species (forbs and graminoids) composition of the soil seed bank based on Tamura (2010, 2019).

26.2 Methods

26.2.1 Study Site

The study was conducted in an old-growth damp beech forest on the northern slope of Mt. Tanzawa in the Tanzawa Mountains. The study site is identified as *Miricacalio-Fagetum crenatae* forest with the tall forb types in the floor and is dominated by deciduous trees such as *Acer shirasawanum*, *Fagus crenata*, *Pterocarya rhoifolia*, and *Acer mono* var. *trichobasis*. The study site ranges from 1500 to 1560 m elevation and from 19° to 23° inclination and is situated on an east to northeast facing slope. The floor vegetation consists of tall forbs, such as *Ligularia dentata* and *Aster leiophyllus* var. *leiophyllus*. The Kanagawa Prefectural Government designated this site a special protection area of Tanzawa-Oyama Quasi-National Park in 1965 because it comprised mostly old-growth temperate deciduous forest. Sika deer (*Cervus nippon*) inhabited the study area in the 1960s but appeared to have no or very little impact on the floor vegetation (Miyawaki et al. 1964). Damage of the floor vegetation caused by sika deer herbivory has occurred since the late 1980s (Furubayashi et al. 1997). The density of sika deer ranged from 6 to 57 individuals km^{-2} between 1996 and 2013 (Kanagawa Prefecture 2017). The deer herbivory brought a notable change in the composition of plant species (Ohno and Ozeki 1997). Certain herbaceous plants, such as *Miricacalia makinoana*, became endangered in Kanagawa Prefecture (Red Data Research Group of Kanagawa 1995). To protect these plants, the Kanagawa Prefectural Government first established five exclosures, 1.8 m high and mesh size 10 cm × 10 cm, on the study site in 1997 (hereafter, E1997) and established seven more exclosures close to E1997 in 2003 (hereafter, E2003). The size of the exclosures ranged from 30 m × 30 m to 45 m × 45 m. Thus, the study sites of E1997 and E2003 have suffered severe deer grazing pressure for ca. 10 years and ca.16 years, respectively, until the exclosures had been established. The area outside of the exclosures has remained degraded floor vegetation for over 20 years.

26.2.2 Tall Forbs

Three exclosures of five E1997 and four exclosures of seven E2003 were selected for analyses after omitting broken exclosures and exclosures with different elevation. The exclosures shared similar topography (i.e., elevation, slope direction, and incline) and belonged to the same vegetation type (*Miricacalio-Fagetum crenatae* forest) before establishing exclosures, judging from two vegetation maps (Miyawaki et al. 1964; Ohno and Ozeki 1997); therefore, the primary conditions among the exclosures were almost similar except for chronic deer herbivory. I targeted 12 tall forb species, 6 of which are endangered species due to deer grazing in Kanagawa Prefecture (Katsuyama et al. 2006). They are defined as perennial herbs with tall stems (>30 cm in height) or broad leaves and were sensitive to deer grazing. All the tall forbs live in and around the damp beech forests of the Tanzawa Mountains.

I and trained field assistants quartered inside E1997 and E2003 in summer following five years of deer exclusion, i.e., in 2002 of E1997 and 2008 of E2003, and made a persistent effort to find the target species. I assumed that a period of five years could be sufficient for the emergence of tall forbs based on my preliminary study (record of flora inside the exclosures). If the forbs were found, the densities of ramets and status (mature or immature) of the forbs were recorded. The status of forbs was judged from the presence or absence of blossoms or fruits. There was little difference between the temperatures of the growing season in 2002 and 2008, indicating that the temperature did not influence the emergence of 12 forbs (Tamura 2010).

26.2.3 Soil Seed Bank

I set up each 20 × 25 m^2 plot inside one of the E1997 and one of the E2003 and outside the exclosures (hereafter, OUT). The exclosure of E1997 is 4 m away from that of E2003, and the E2003 is 5 m away from the OUT plot. Each exclosed plot was >5 m away from the exclosure to avoid edge effects. Study plots were divided into 20 (5 × 5 m^2) subplots; one 2 × 2 m^2 quadrat was established inside each subplot, and one smaller 20× 20 cm^2 subquadrat was established adjacent to the quadrat. A detailed protocol is shown in Tamura (2019).

The cover class of each herb species in each quadrat was recorded using the Braun-Blanquet scale (Braun-Blanquet 1964) in July 2008. The scientific nomenclature of all plant species follows *Flora Kanagawa 2018* (Flora Kanagawa Association 2018).

The seed bank was sampled before spring germination on April 16 and 21, 2008. Surface soil samples of each of the 20 subquadrats (20 cm × 20 cm × 5 cm depth) inside E1997, E2003, and OUT were carefully collected using a shovel. Collected samples were immediately taken to the Kanagawa Prefecture Natural Environment Conservation Center in Atsugi City and spread out in a thin layer (2 cm) in plastic containers (Yamato C type), each with an area of 784 cm^2. Emergent seedlings were marked with color-coded and labeled toothpicks every 3–7 days and were removed after identification. This procedure was carried out for approximately 150 days after the incubation started, from late April to late September. No seedling germination was checked the following year. No seedlings germinated in the control containers. Germinated seedlings with cotyledons were considered current year seedlings, and those of herb species (forbs and graminoids) except woody plants were used for analysis. Small tiny weed seedlings such as *Gnaphalium affine* and *Youngia japonica*, which grew outside the greenhouse but not at the study site, occurred in the containers and were not used for analysis.

26.2.4 Data Analysis

The Mann-Whitney U-test was performed on the difference of tall forb numbers between E1997 and E2003 with a corrected area. A Steel-Dwass test was performed on the difference of cover of aboveground herb species among E1997, E2003, and OUT. Vulnerable (VUL) species to deer grazing were defined when the cover was E1997 > E2003 and/or OUT, both E1997 and E2003 > OUT. Invulnerable (INV) species was defined when the cover was OUT > E1997 and/or E2003, both E2003 and OUT > E1997, VUL species are so-called palatable, and INV species are so-called unpalatable or grazing tolerant, which includes species that can produce seeds even after being grazed by deer. Remnant species were defined as other species. Relative dominance in soil seed banks was calculated using the number of buried seeds with VUL and INV species and forest forb species and others. Forest forb species were followed by the description of habitat in *Flora Kanagawa 2018*. A Steel-Dwass test was also performed on the difference of soil seed densities among E1997, E2003, and OUT. These analyses were conducted by MEPHAS (http://www.gen-info.osaka-u.ac.jp/MEPHAS/).

26.3 Results

26.3.1 Density of 12 Forbs inside the Exclosures Established in 1997 and 2003

Nine to eleven species were present in E1997, and five to six species were present in E2003 though the area of each exclosure differed with one another (Table 26.1). Densities of four species, such as *Anemonopsis macrophylla* and *Polygonatum macranthum*, were significantly greater in E1997 than in E2003 (Table 26.1, Mann-Whitney U-test, $p < 0.05$). There was no significant difference for another eight species between E1997 and E2003. The ratio of mature ramets to all ramets of species tended to be higher in E1997 than in E2003 for *Cimicifuga japonica* and *Parasenecio maximowiczianus*; in contrast, the ratio tended to be higher in E2003 than in E1997 for *Saussurea hisauchii* and *Trillium apetalon*. For the three species that occurred only in E1997, the ratio of *Lilium medeoloides* was high, but the ratio of *Anemonopsis macrophylla* and *Miricacalia makinoana* was low (Fig. 26.1).

26.3.2 Soil Seed Bank inside the Exclosures Established in 1997 and 2003 and outside the Exclosures

Six herb species were identified as VUL species, and eight were identified as INV species based on the analyses for aboveground herb coverage (Table 26.2). One of six VUL species and five of eight INV species were germinated from the seed banks inside and outside the exclosures. Total species richness ($0.80\ \mathrm{m}^{-2}$) and total density of buried seeds were most remarkable in E2003 among the three plots (Table 26.3a). The seed density of VUL species was $1.3\ \mathrm{m}^{-2}$ only in E1997. The species is *Polygonatum macranthum*, which is 1 of the 12 tall forb species targeted for the aboveground survey. In contrast, the seed density of INV species was many in three plots and was most remarkable in E2003, followed by OUT (Table 26.3a). Relative

Table 26.1 Density of 12 tall forb species inside 2 exclosures, which differ in established year, in a damp beech forest (revised from Tamura 2010)

Species name	Habitat Type	2006 RD Lank	E1997				E2003					P value
			1997a 0.12 ha	1997b 0.20 ha	1997c 0.16 ha	Total 0.48 ha	2003a 0.16 ha	2003b 0.16 ha	2003c 0.16 ha	2003d 0.16 ha	Total 0.64 ha	
Anemonopsis macrophylla	FF	1B	1	8	1	10	0	0	0	0	0	0.018*
Cimicifuga japonica	FF	–	1	8	21	30	57	5	0	0	62	0.476
Hydrangea alternifolia	FF	–	11	5	300	316	600	220	4	12	836	0.724
Lilium medeoloides	FF	1A	0	8	11	19	0	0	0	0	0	0.078
Maianthemum robustum	FF	1B	33	77	16	126	0	6	1	5	12	0.034*
Miricacalia makinoana	FF	1B	4	0	0	4	0	0	0	0	0	0.248
Parasenecio maximowiczianus	FF	–	157	39	3	199	0	0	1	0	1	0.028*
Polygonatum macranthum	FF	–	22	145	77	244	8	7	19	16	50	0.034*
Rubia chinensis	FF	1A	0	0	1	1	3	0	0	0	3	1.000
Saussurea hisauchii	Other	–	0	62	12	74	0	3	0	0	3	0.172
Spuriopimpinella koreana	FF	1B	9	24	1	34	5	0	8	13	26	0.373
Trillium apetalon	FF	–	12	15	5	32	0	2	3	27	32	0.289
Species number			9	10	11	12	5	6	6	5	9	

E1997 inside the exclosure fence established in 1997, *E2003* inside the exclosure fence established in 2003, *FF* forest floor, $*p < 0.05$

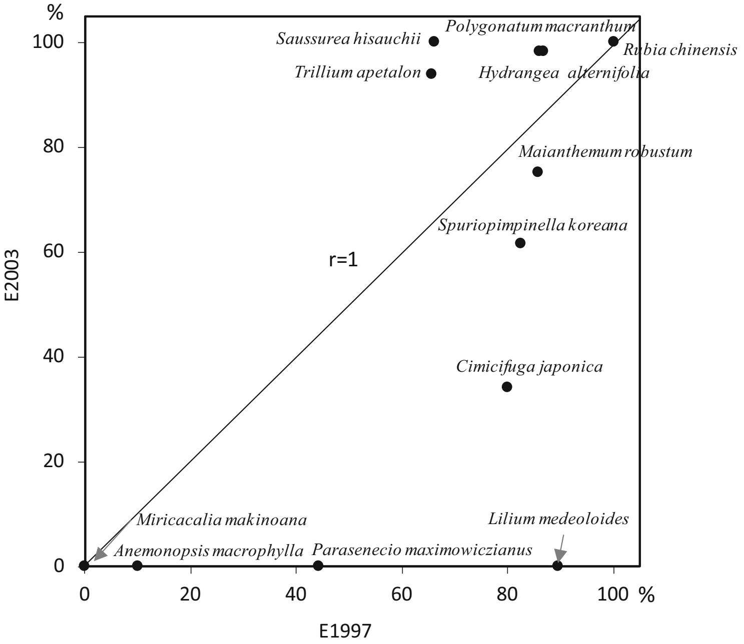

Fig. 26.1 Ratio of matured ramets to total ramets of tall forb species between exclosures established in 1997 and 2003 (revised from Tamura 2010). *E1997* inside the exclosure established in 1997, *E2003* inside the exclosure established in 2003

dominance of VUL and INV species was similar between E2003 and OUT, but that of E1997 was different from E2003 and OUT (Table 26.3a).

At the species level, *Aster leiophyllus* var. *leiophyllus* and *Pilea hamaoi*, both of which are INV species, emerged in great numbers in all three plots (Table 26.4). *Hydrocotyle yabei* (INV), annual *Pilea hamaoi* (INV), *Persicaria debilis*, and *Persicaria nepalensis* were significantly greater in E2003 than in E1997 and OUT (Table 26.4). The large perennial *Ligularia dentata* (INV) was significantly greater in OUT than in E1997 and E2003. The species targeted for the aboveground survey do not emerge from soil seed bank at all except for *Polygonatum macranthum.*

The species richness and the density of forest forb species were also most abundant in E2003; however, the relative dominance of forest forb species was highest in E1997 followed by E2003 (Table 26.3b).

Table 26.2 List of vulnerable and invulnerable species to deer grazing determined from statistical significance of the mean cover of floor vegetation among two exclosures established in 1997 and 2003 and outside the exclosures (revised from Tamura 2019)

Type	Habitat type	Life form	Species name	Mean cover (%)		
				E1997	E2003	OUT
Vulnerable (VUL)	Other	MP	*Athyrium yokoscense*	3.65^{a}	0.31^{b}	0.08^{ab}
	FF	SP	*Carex fernaldiana*	0.58^{a}	0^{b}	0^{b}
	FF	MP	*Cimicifuga japonica*	0.56^{a}	0^{b}	0^{b}
	FF	MP	*Leucosceptrum japonicum*	2.87^{a}	0.01^{b}	0.04^{ab}
	FF	LP	*Maianthemum robustum*	0.57^{a}	0^{b}	0^{b}
	FF	LP	*Polygonatum macranthum*	0.88^{a}	0.01^{b}	0.01^{b}
Invulnerable (INV)	FF	MP	*Aster leiophyllus* var. *leiophyllus*	4.54^{b}	12.80^{ab}	15.70^{a}
	FF	MP	*Brachypodium sylvaticum*	0.55^{b}	0.01^{b}	1.49^{a}
	Other	SP	*Carex aphanandra*	0.01^{ab}	0^{b}	0.03^{a}
	FF	SP	*Dichocarpum stoloniferum*	0.07^{b}	2.64^{ab}	3.13^{a}
	FF	SP	*Hydrocotyle yabei*	0.01^{b}	0.62^{a}	0.05^{a}
	Other	LP	*Ligularia dentata*	13.83^{b}	10.61^{b}	36.55^{a}
	Other	SP	*Muhlenbergia japonica*	0^{b}	0^{b}	0.03^{a}
	Other	A	*Pilea hamaoi*	0^{b}	0.06^{a}	0.06^{a}

E1997 inside the exclosure established in 1997, *E2003* inside the exclosure established in 2003, *OUT* outside the exclosures, *FF* forest floor, *LP* large perennial, *MP* medium perennial, *SP* small perennial, *A* annual. Different letters are significantly different at $p < 0.05$

26.4 Discussion

26.4.1 Difference in Density of Forbs Following Exclusion of Deer under Different Periods of Chronic Herbivory

The aboveground study revealed that densities of four forb species were significantly greater in E1997 than in E2003 (Table 26.1) and that the ratio of mature ramets to all ramets of *Cimicifuga japonica* tended to be higher in E1997 than in E2003 (Fig. 26.1). These results suggested that the 6-year different periods of chronic deer herbivory before the exclosures were established caused delay of recovery in tall forbs densities or decreased densities in E2003. On the other hand, the ratio of mature ramets to all ramets of *Anemonopsis macrophylla* and *Miricacalia makinoana* was very low compared to that of another species in E1997, probably because chronic deer herbivory remained even in E1997. Such species might need more extended periods to mature. For example, *Anemonopsis macrophylla* needs more than ten years to mature (Suzuki and Kimura 2007). In the 1960s, *Miricacalia makinoana* had been dominant or frequent enough to be selected as characteristic species in damp beech forests (*Miricacalio-Fagetum crenatae*) of the Tanzawa Mountains (Miyawaki et al. 1964). The species was presently scarce, and no mature

Table 26.3 Herb species richness and its seed density of soil seed bank based on vulnerability and habitat (revised from Tamura 2019)

	Species richness (0.8 m^{-2})			Seed density (m^{-2})		
Type	E1997	E2003	OUT	E1997	E2003	OUT
(a) Vulnerability type						
Vulnerable (VUL)	1	0	0	1.3 (0.3%)	0.0 (0.0%)	0.0 (0.0%)
Invulnerable (INV)	5	6	6	200.2 (42.5%)	1051.4 (69.1%)	396.5 (69.3%)
Other	19	26	17	269.4 (57.2%)	469.7 (30.9%)	175.5 (30.7%)
Total	25	32	23	470.9 (100.0%)	1521.1 (100.0%)	572.0 (100.0%)
(b) Habitat type						
Forest floor (FF)	11	16	11	216.6 (46.0%)	538.1 (35.4%)	187.8 (32.8%)
Other	14	16	12	254.3 (54.0%)	983.0 (64.6%)	384.2 (67.2%)
Total	25	32	23	470.9 (100.0%)	1521.1 (100.0%)	572.0 (100.0%)

E1997 inside the exclosure fence established in 1997, *E2003* inside the exclosure fence established in 2003, *OUT* outside the exclosure fences

Table 26.4 Herb species composition of the soil seed bank inside two exclosures established in 1997 and 2003 and outside the exclosures in a beech forest (revised from Tamura 2019)

Type	Habitat type	Life form	Species name	Seed density (m^{-2})		
				E1997	E2003	OUT
VUL	FF	LP	*Polygonatum macranthum*	1.3	0	0
INV	Other	MP	*Aster leiophyllus* var. *leiophyllus*	105.0	175.0	170.0
INV	FF	SP	*Dichocarpum stoloniferum*	0	1.3	1.3
INV	FF	SP	*Hydrocotyle yabei*	1.3^{b}	163.8^{a}	36.3^{b}
INV	Other	LP	*Ligularia dentata*	8.8^{b}	5.0^{b}	31.3^{a}
INV	Other	A	*Pilea hamaoi*	83.8^{b}	698.8^{a}	156.3^{b}
	Other	LP	*Aconitum japonicum* subsp. *japonicum*	31.3^{a}	26.3^{a}	0^{b}
	Other	MP	*Aster microcephalus* var. *ovatus*	1.3	1.3	0
	FF	MP	*Astilbe thunbergii* var. *thunbergii*	3.8	2.5	0
	FF	SP	*Cardamine anemonoides*	7.5	15.0	7.5
	Other	MP	*Carex multifolia*	3.8	0	0
	FF	SP	*Circaea alpina*	1.3	11.3	12.5
	FF	SP	*Circaea erubescens*	15.0	8.8	5.0
	FF	LP	*Cirsium tenuipedunculatum*	38.8	56.3	10.0
	FF	MP	*Clinopodium micranthum* var. *micranthum*	106.3^{a}	83.8^{a}	16.3^{b}
	Other	MP	*Cynoglossum furcatum* var. *villosulum*	1.3	0	0
	Other	MP	*Epilobium amurense*	1.3	2.5	1.3
	Other	MP	*Eupatorium makinoi* var. *oppositifolium*	1.3	0	0
	Other	MP	*Festuca parvigluma*	1.3	7.5	1.3
	Other	SP	*Galium paradoxum* subsp. *franchetianum*	0	0	7.5
	FF	MP	*Galium pseudoasprellum*	0	7.5	2.5
	FF	SP	*Geranium tripartitum*	0	1.3	1.3
	FF	MP	*Geum japonicum* var. *japonicum*	1.3^{a}	36.3^{ab}	0^{b}
	Other	SP	*Hosta longipes*	1.3	2.5	2.5
	Other	MP	*Laportea bulbifera*	1.3	1.3	0
	Other	A	*Panicum bisulcatum*	0	1.3	0
	FF	MP	*Parasenecio delphiniifolius*	2.5	0	0
	FF	SP	*Peracarpa carnosa*	0	1.3	1.3
	Other	A	*Persicaria debilis*	10.0^{b}	38.8^{a}	1.3^{b}
	Other	A	*Persicaria longiseta*	0	2.5	0
	Other	A	*Persicaria nepalensis*	0^{b}	13.8^{a}	0^{b}
	FF	MP	*Physaliastrum japonicum*	0	1.3	0
	Other	A	*Pilea japonica*	0	3.8	1.3
	Other	SP	*Plantago asiatica* var. *asiatica*	0	1.3	1.3
	FF	SP	*Pseudostellaria heterantha*	0	1.3	0
	FF	MP	*Sanicula chinensis*	0	10.0	0

(continued)

Table 26.4 (continued)

Type	Habitat type	Life form	Species name	Seed density (m^{-2})		
				E1997	E2003	OUT
	FF	SP	*Veronica miqueliana*	37.5^{b}	136.3^{a}	93.8^{ab}
	Other		*Arisaema* sp.	0	0	1.3
	Other		*Liliaceae* sp.	2.5	1.3	0
	Other		Unidentified	0	0	8.8

E1997 inside the exclosure established in 1997, *E2003* inside the exclosure established in 2003, *OUT* outside the exclosures, *FF* forest floor, *LP* large perennial, *MP* medium perennial, *SP* small perennial, *A* annual; different letters are significantly different at $p < 0.05$

individuals even inside E1997 (Table 26.1, Fig. 26.1), suggesting that establishing E1997 could be too late to restore the species.

This study adds to the understanding of the effect of chronic deer herbivory on forest forbs in Japan, which has been seldom studied until now. Several studies have reported that forbs did not recover as expected even after exclosures were established (Augustine and Frelich 1998; Fletcher et al. 2001; Habeck and Schultz 2015; Webster et al. 2005). Augustine and Frelich (1998) indicated that if grazing intensities observed at sites with high deer density (25–35 km^{-2}) continue for more than 15–20 years, the deer can drive the *Trillium grandiflorum* population to local extinction. Webster et al. (2005) reported that recovery consisted mainly of an increase in survivors with little or no recolonization by browsing-sensitive species following eight years of deer exclusion at a site impacted by deer for 17–18 years at a density that peaked at 43 km^{-2}. In this study, there was a difference between forbs densities after about 10 and 16 years of chronic deer herbivory (Table 26.1), indicating that the density of tall forbs could decline gradually under continuous chronic deer herbivory. These results demonstrate that it is difficult to recover for forbs heavily grazed by sika deer to their former level over time, even after establishment of exclosures.

This study was conducted following five years of deer exclusions both in E1997 and E2003. Forb species that were none or scarce in E2003 may emerge on the ground over time if the plant organs like bulb or tuber were alive in the ground, and this is the next problem to be solved.

26.4.2 Difference in Herb Species Composition of Soil Seed Banks Following Exclusion of Deer under Different Periods of Chronic Herbivory

This seed bank study revealed that 1 individual of VUL species (*Polygonatum macranthum*), which is 1 of the 12 forb species I targeted for the aboveground study, emerged only in E1997; by contrast, many INV species emerged in the three plots (Tables 26.3 and 26.4), indicating that it is difficult for VUL species to form buried seed banks and that INV species can easily form buried seed banks. The other 11 species except for *Polygonatum macranthum* targeted for the aboveground study were not germinated from soil seed banks. Previous studies reported that forest forbs do not form buried seed banks and instead propagate clonally (Bossuyt et al. 2002; Leckie et al. 2000; Pickett and McDonnell 1989). However, the seedlings of forest forb species, whose habitat type is forest floor, in this study germinated 188–538 m^{-2} and 33–46% in relative dominance in the three plots (Table 26.3). These results suggest that no forest forbs do not form soil seed banks but VUL forb species may be difficult to form soil seed banks.

The seed bank study also revealed that the relative dominance of INV species was higher in E2003 and OUT than in E1997 and relative dominance of forest forbs was lower in OUT followed by E2003 than in E1997 (Table 26.3), indicating that INV species increased in E2003. Numerous seedlings of INV species, such as *Aster leiophyllus* var. *leiophyllus* and *Pilea hamaoi*, germinated in the three plots (Table 26.4). Additionally, the germinated seedlings of INV species, such as *Hydrocotyle yabei* and *Pilea hamaoi*, and annual herbs, such as *Persicaria debilis* and *Persicaria nepalensis*, were more significant in E2003 than in E1997 and OUT (Table 26.4). These species were greater in E2003 than in OUT because the species were grazed by deer in OUT, thereby causing a decline in seed production and input into the soil. These results suggest that different periods of chronic deer herbivory could affect INV herb species of soil seed bank.

Previous studies have reported that restoration of forbs from soil seed banks under a mature natural forest might be unrealizable (Bossuyt and Honnay 2008; Halpern et al. 1999; Tamura 2016). Halpern et al. (1999) indicated that possibilities for restoring native communities through seed banks are severely limited, even where there are no or few deer. Bossuyt and Honnay (2008) summarized that the probability of successful restoration for forest forbs remains very small for an extended period and that restoration based on the seed bank is only possible at sites that were degraded less than five years prior. This study revealed that VUL herb species could seldom form buried seed banks, but plenty of forest forbs, not VUL species, can form seed banks, as mentioned above. Accordingly, restoration of tall forbs, especially VUL forbs, cannot rely only on seed germination from the soil seed bank despite chronic deer herbivory.

26.5 Conclusion

This chapter provides insight into the effect of chronic deer herbivory on both tall forbs and soil seed banks of herb species. I particularly demonstrate that chronic deer herbivory causes a negative effect on tall forb densities in aboveground and a positive effect on the seed density of INV species through soil seed banks. This review revealed the reason why retrogressed floor vegetation by deer for a prolonged period is difficult to recover after conducting conservation measures, such as establishing exclosures or controlling deer (Habeck and Schultz 2015; Tanentzap et al. 2012), while forb species that form buried soil seed banks, including INV species, can spread its distribution under deer herbivory or after controlling deer. These findings indicate that if vulnerable forbs to deer grazing disappear aboveground, they cannot recover the following declines in deer population without new seed dispersal. Accordingly, to conserve vulnerable forests composed of the forb-dominated floor, conservation measures are needed during the period when the organs of the plant still remain in the aboveground.

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Chapter 27

Indirect Effects of Deer Overgrazing on Stream Ecosystems

Masaru Sakai, Keitaro Fukushima, and Hikaru Nakagawa

Abstract Understory vegetation in forests retains nitrogen and mitigates soil runoff. Deer overgrazing impairs these ecosystem functions and thus indirectly affects aquatic environments. This chapter summarizes the state of knowledge of overgrazing effects on forested streams of headwater to downstream (first- to fourth-order streams). A 10-year monitoring program assessed water chemistry in an exclosure catchment (EC) and a control catchment (CC) and found that deer-induced understory degradation related to increased exports of nitrate and suspended sediments from hillslopes to streams. Four years after the construction of the EC's deer-exclusion fence, sedimentation and a macroinvertebrate community dominated by burrowers were observed in the first-order streams in the CC, but not in the second-order streams. Eleven years of fish community monitoring in a fourth-order stream documented an increase in a benthic fish species and a simultaneous decrease in a water-column-dwelling species that preferentially utilizes pebble-cobble-dominated streambeds for spawning. Together, these results show that the magnitude of overgrazing impacts varies both spatially and temporally as a result of sediment transport and deposition processes. Our results emphasize the importance of catchment-scale ecosystem-management approaches and an interdisciplinary approach that includes ecology, hydrology, and fluvial geomorphology in mitigating the impacts of overgrazing on stream ecosystems.

M. Sakai (✉)
Fukushima Regional Collaborative Research Center, National Institute for Environmental Studies, Miharu, Japan
e-mail: sakai.masaru@nies.go.jp

K. Fukushima
Center for Ecological Research, Kyoto University, Otsu, Japan
e-mail: ktaro.f@gmail.com

H. Nakagawa
Center for Southeast Asian Studies, Kyoto University, Kyoto, Japan
e-mail: hikarunakagawa@icloud.com

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27.1 Introduction

Overgrazing by deer has been reported from ecosystems around the world (Côté et al. 2004). Deer damage crops (VerCauteren et al. 2006) and impair native plant communities (Rooney 2001; Casabon and Pothier 2008; Chaps. 3, 19, and 25). In the latter case, overgrazing may lead to decrease understory vegetation cover and promote soil erosion (Sakai et al. 2012), which may then have indirect effects on ecosystem physicochemical and biological properties. It is therefore critical to evaluate the full range of direct and indirect impacts of overgrazing for developing and enacting appropriate ecosystem-level management and conservation strategies.

Sika deer (*Cervus nippon*) are increasing throughout Japan due in part to more moderate winter conditions, decreased hunting pressure, and tighter hunting laws (McCullough et al. 2009). The increasing deer populations are related to a reduced density of palatable plant species, as well as reduced overall diversity (Nakahama et al. 2020). Understory vegetation has various ecosystem functions; it provides habitat and food resources for other biotas, maintains the infiltration capacity of soil, and retains nitrogen (Sakai 2013). Deer overgrazing leads to impairment of these important processes (Sakai et al. 2012; Sakata and Yamasaki 2015; Furusawa et al. 2016).

The effects of deer overgrazing may permeate the boundary separating forest and stream ecosystems through interdependencies and interactions between hydrological and ecological processes. For example, overgrazed understory vegetation has less ability to retain biological nitrogen, which can then lead to elevated nitrate concentrations in streams (Fukushima et al. 2013, 2014). Soil runoff from hillslopes delivers fine sediments, impacting macroinvertebrates in headwater streams (Sakai et al. 2012, 2013). Introduced sediments may also be transported and later deposited in slow-flowing areas in larger-order streams, affecting fish communities (Nakagawa 2019a).

In this chapter, we discuss the findings of field research to assess the indirect effects of overgrazing by Sika deer in the upper reach stream ecosystems of the Yura River, Kyoto, Japan. We broadly discuss the permeation of terrestrial overgrazing effects into aquatic ecosystems.

27.2 Methods

27.2.1 Study Site

Our study was conducted at the Ashiu Forest Research Station of the Field Science Education and Research Center, Kyoto University (41.9 km^2, 35°20′N, 135°45′E) (Fig. 27.1a). The mean (± standard deviation [SD]) annual precipitation and temperature and maximum snow depth at the research station were 2396 ± 309 mm, 12.2 ± 0.6 °C, and 1.01 ± 0.40 m, respectively, in the period 1998–2018 (Nakagawa

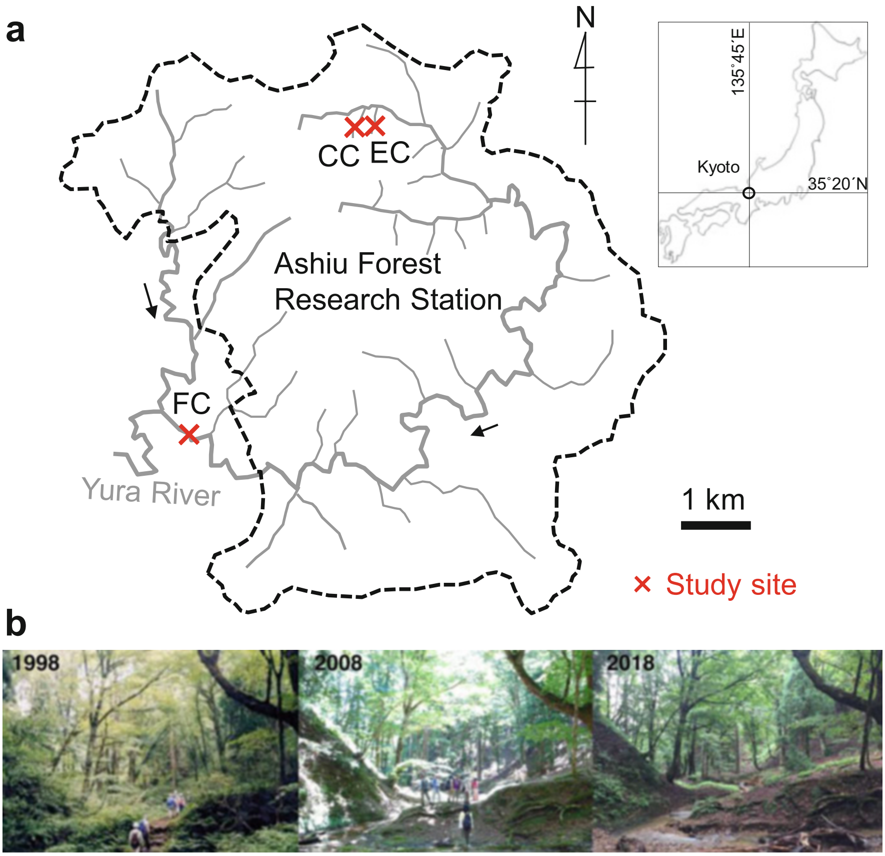

Fig. 27.1 (**a**) Study site at Ashiu Forest Research Station, Kyoto, Japan. The deer-exclosure catchment (EC) and control (CC) catchment are drained by the second-order streams. These catchments were used for macroinvertebrate and water-chemistry assessments. Fish surveys were conducted downstream in a fourth-order stream of the fish catchment (FC). (**b**) Images of the same location at Ashiu Forest Research Station in 1998, 2008, and 2018, from Nakagawa (2019a). The left and center photos were taken by S. Shibata and T. Yoshioka and were provided by the Field Science Education and Research Center, Kyoto University

et al. 2020). The soils are typical brown forest soils, and the area is underlain by sandstone, mudstone, and shale of the Mesozoic Tanba Belt. The study area is dominated by primary and secondary temperate forests and conifer plantations; <0.02 km^2 of the area at the lowest elevations is subject to residential or agricultural use (Nakagawa 2019a). >0.01 km^2 clear-cut logging has not been performed in recent 30 years in the forest.

Overgrazing by deer has been a serious problem in the study area since the late 1990s (Tanaka et al. 2008) and has led to a decline in understory plant abundance and diversity (Kato and Okuyama 2004) (Fig. 27.1b). A decade of population estimates (2007–2018) suggests that deer density peaked at 71.0 individuals/km^2

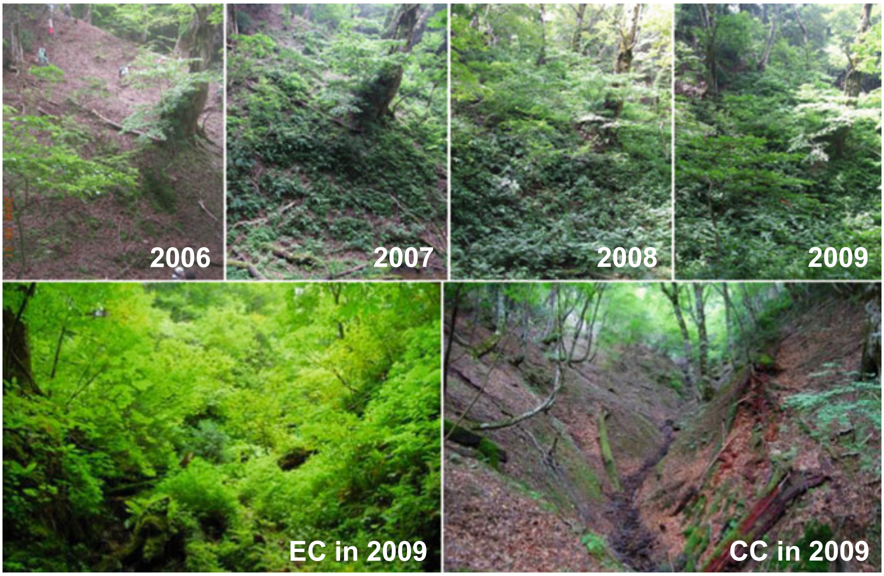

Fig. 27.2 Images showing vegetation recovery inside the deer-exclosure catchment from 2006 to 2009 (upper panel) and in the deer-exclosure and control catchments in 2009 (lower panel), from Sakai et al. (2013). Photographs were taken during the summer

in 2010 and then decreased by at least 10 individuals/km^2 as a result of nuisance-control measures (Mizuki et al. 2020).

In June 2006, an exclusion fence to prevent deer grazing was constructed around a catchment area (exclosure catchment [EC]; 0.13 km^2) that drains to a second-order stream (Fig. 27.2). A 2.5-m-high fence was constructed of poles and nets along the ridge line of the entire catchment. Continual maintenance of the fence ensured that deer did not enter the catchment, but the fence was lowered during the winter to avoid breakage due to accumulated snow. We established a control catchment (CC; 0.19 km^2) adjacent to the EC. The elevation range and orientation of the two catchments were extremely similar. Both catchments are dominated by primary cool-temperate forest with *Fagus crenata*, *Aesculus turbinata*, *Pterocarya rhoifolia*, and *Cryptomeria japonica* var. *radicans*. We assessed the impact of deer overgrazing on water chemistry and macroinvertebrates in streams (Sakai et al. 2012, 2013; Fukushima et al. 2013, 2014) in these catchments. Fish were investigated in a connected fourth-order stream within a fish catchment area (FC; 36.5 km^2) (Nakagawa 2019a) (Fig. 27.1a).

27.2.2 Soil and Water Chemistry

Following exclosure construction, we collected stream water samples monthly to bimonthly under base-flow conditions at the catchment outlets for a decade. Water samples were filtered through a syringe filter with a 0.45 μm pore size membrane (25CS045AN, Advantec Toyo Kaisha, Ltd., Tokyo, Japan), and the nitrate concentration was determined using ion chromatography (ICS-90, Dionex, CA, USA). Studies have suggested that, in forested catchments, temporal variation in stream water chemistry during storm events is greater than seasonal variation under base-flow conditions (Ohrui and Mitchell 1999; Dhillon and Inamdar 2014). Episodic pulses of nitrate and particle materials released during large storm events can substantially contribute to annual nitrogen and sediment exports from terrestrial to aquatic systems. Thus, in addition to base-flow sampling, we took stream samples under storm-flow conditions from September 2010 to September 2011. Storm-event sampling was performed every 2 h during storm-flow periods using an automated portable sampler (ISCO 3700, Teledyne Technologies, CA, USA), which was manually turned on prior to the expected arrival of a storm. Storm-flow water samples were filtered through a precombusted (500 °C for 4 h) 0.7 μm glass-fiber filter (GF/F, Whatman, Maidstone, UK) within 24 h of collection. The weight of suspended sediments (SSs), including particulate organic matter (POM), on the filter was determined after drying at 80 °C for 24 h. We determined POM concentration using a loss-on-ignition method (450 °C for 4 h). The concentrations of SSs and POM were obtained by dividing their respective dry weights by the sample volume. Filtrates were then filtered through a 0.45 μm membrane prior to measuring inorganic nitrogen concentration. For each storm event, flow-weighted mean concentration (C_m) was estimated as follows for SSs, POM, and nitrate:

$$C_m = \sum_{i=1}^{n} C_i \cdot Q_i / \sum_{i=1}^{n} Q_i$$

where C_i is the measured concentration and Q_i is the corresponding stream flow discharge value at time *i*.

Hydrological conditions during storm events were assessed as the total amount of precipitation during the storm event, the sum of precipitation for the 7 days prior to the event, total stream discharge during the event, and the ratio of direct runoff to total discharge. We estimated direct runoff using the method of Hewlett and Hibbert (1967).

Understory vegetation cover was assessed annually in a 20 × 40 m quadrat located on a lower slope near the stream that ran through both catchments (Sakaguchi et al. 2012). Soil surveys were conducted from September to November 2008 (Fukushima et al. 2014). We established 4-m-wide transects along the valley and placed quadrats at 10 m intervals along their length in both the EC and CC. Humic-layer depth (FH) was measured at four points within each quadrat and then averaged. Mineral soil (0–5 cm in depth) was collected at these same four points using a 100 mL core sampler and pooled to form a composite sample for each quadrat. Soil samples were immediately taken to the laboratory, sieved through a 2 mm sieve, and divided into four subsamples for the following measurements. Each subsample was dried at 105 °C for 48 h to estimate soil water content. Ammonium and nitrate concentrations were determined by extracting subsamples with a 2 M potassium chloride (KCl) solution. Subsamples were incubated in the dark for 4 weeks at 25 °C at the initial water content level. The net production rates of inorganic nitrogen (ammonium + nitrate; mineralization rate) and nitrate (nitrification rate) were then determined using extraction with KCl. Finally, the samples were dried at 40 °C for a week and then ground to determine carbon and nitrogen concentrations using an NC analyzer (Sumigraph NC-22A, Sumika Chemical Analysis Service, Ltd., Tokyo, Japan). Ammonium and nitrate concentrations in the KCl extract were determined using an automated continuous-flow colorimetric method (AutoAnalyzer III, BLTEC, Osaka, Japan).

27.2.3 Macroinvertebrates

We selected four first-order stream reaches and one second-order reach in both the EC and the CC, i.e., five stream study sites per catchment. Perennial 30 m channel reaches downstream were selected to examine in-stream physical conditions (catchment area, water depth, relative photosynthetically active radiation [rPAR], and the proportion of fine-sediment deposition), periphyton biomass, and macroinvertebrate communities (Sakai et al. 2013). The channel reach types in the ten study reaches were colluvial, with limited riffle-pool structures, with dominant substrate types of cobble, gravel, and sand.

Hydrological observations were conducted in one first-order stream in the EC and one in the CC. Stream discharge was measured every 5 min using a 5 inch Parshall flume with a water-level sensor placed at the outlet of each catchment. Discharge was calculated using a calibration equation for stage and discharge. Electrical conductivity was measured every 10 min using an electrical conductivity sensor equipped with a data logger. Rainfall was measured using a tipping-bucket rain gauge located in an open area 200–300 m away from the catchments. The mean conductivity of the rainwater was used as a proxy of the conductivity of overland flow in determining the contribution of overland flow to streams (Sakai et al. 2013).

A canonical correspondence analysis (CCA) was used to assess gradients and identify environmental factors potentially influencing macroinvertebrate communities. Environmental factors included catchment area, water depth, the proportion of fine-sediment deposition, rPAR in August and April, and periphyton biomass. We used mean abundance data for the 50 most abundant macroinvertebrate taxa (which represented 96% of the total number of individuals) for this analysis. The statistical significance of Axis 1 was assessed using a Monte Carlo permutation test with 199 permutations under the full model. We then combined macroinvertebrate communities based on similarity and created several macroinvertebrate community groups from the overall communities of the ten study streams. We then applied an indicator species analysis (Dufrêne and Legendre 1997), using a Monte Carlo permutation test with 199 permutations, to identify species characterizing each macroinvertebrate community group. All statistical analyses were performed using PC-ORD ver. 6 (McCune and Mefford 2011).

27.2.4 Fishes

We monitored fish species and their habitats by snorkeling surveys, using a line-transect method, in 220 m stream sections in the FC from May 2007 to June 2018. We conducted 75 separate fish surveys and 68 habitat surveys, but it should be noted that these were not conducted at strictly regular intervals. We established 22 line transects at 10 m intervals perpendicular to water flow along the channel in the FC. We then established six plots at regular intervals along each transect and assessed microhabitat characteristics, including water depth, current velocity, and the proportions of sand, granule, pebble, cobble, boulder, and bedrock in each plot. Fish surveys were conducted during the day (09:00–15:00) and at night (21:00–03:00). We surveyed the nocturnally active species *Hemibarbus longirostris*, *Pseudogobio esocinus*, *Cobitis* sp., *Liobagrus reinii*, *Cottus pollux*, and *Odontobutis obscura* at night and all other species during the day. Only individuals aged 1 year or older were included in the analysis due to high mortality and field identification challenges for fish <1 year of age. Detailed methodology and data are archived in the Japan Long-Term Ecological Research Network database (JaLTER; ERDP-2018-07, Nakagawa 2019b). We calculated the mean water depth and current velocity and the mean proportion of each streambed substrate type for each survey. We used the total number of individuals of the 13 most numerous fish species observed during each survey for analysis.

Temporal changes in fish populations and stream habitat characteristics were assessed using a state-space model (SSM; Commandeur and Koopman 2007). SSM is a flexible model framework that can accommodate various data types, including population and community dynamics, by two sub-models; one model is the process model that describes the latent population dynamics of fish and its stochasticity, and the other model is the observation model that describes the observation error in relation to the method of observation. Because measurements of habitat characteristics were not completed for all of the observations and the periods between observations were not entirely consistent, missing observation values were estimated when an observation did not have complete environmental data or when a period of non-observation was 2 months or longer.

Process equation was assumed to follow a normal distribution in the SSM:

$$\mu_t \sim \text{Normal}\left((1+c)\,\mu_{t-1}, {\sigma_\mu}^2\right) \tag{27.1}$$

where c is a constant to examine the directional change of habitat characteristics (Y) that was preliminarily assumed, μ_t is the mean habitat state at time t, and σ_μ is the standard deviation of the mean habitat state. A normal error distribution was assumed for the mean and SD of water depth and current velocity as:

$$Y_t \sim \text{Normal}\left(\mu_t + S_t, {\sigma_Y}^2\right) \tag{27.2}$$

where S_t is the seasonal adjustment at time t and σ_Y is the standard deviation of observation errors. A six-step seasonal cycle was assumed as the seasonal adjustment in the SSM following Commandeur and Koopman (2007). A beta error distribution was assumed for the mean proportion of each substrate. Then, the process errors were assumed as:

$$\log\ (\mu_t) \sim \text{Normal}\left(\log\ (1+c) + \log\ (\mu_{t-1}), {\sigma_\mu}^2\right) \tag{27.3}$$

because the mean proportion of each substrate was described using the inverse-logit link function as:

$$Y_t \sim \text{Beta}\ (a, b) \tag{27.4}$$

$$a = \text{inv\_logit}\ (\mu_t + S_t)\ \varphi_Y \tag{27.5}$$

$$b = (1 - \text{inv\_logit}\ (\mu_t + S_t))\ \varphi_Y \tag{27.6}$$

where φ_Y is a divergence parameter.

The process of temporal changes in fish populations was described using the Gompertz population model, a log-linear form of discrete logistic equation function (Royama 1992; Turchin 2003; Fukaya et al. 2013):

$$\log\ (\lambda_t) \sim \text{Normal}\left(r_s + (1-d)\ \log\ (\lambda_{t-1}), {\sigma_\lambda}^2\right) \tag{27.7}$$

where λ_t is the mean state of a fish population at time t, σ_λ is the standard deviation of the mean state of a fish population, r_s are the season-specific rate of increase of a fish population in season s at time $t-1$, and d are the density dependence, respectively (Royama 1992; Turchin 2003; Fukaya et al. 2013). Season-specific parameters were assumed for the rate of increase of a fish population, because the focal fish species are known to have clear seasonality in breeding and growth (Nakamura 1969; Kawanabe and Mizuno 2001). As in the model of habitat changes, missing observation values were estimated for periods of 2 months or longer that held no observations, and a six-step seasonal cycle was assumed. In this model, the six-step seasonal cycle may represent a season-specific factor that is not related to population growth of fishes but effects on the count of fishes such as the finding rate of the individuals of fishes in a snorkeling observation in each season. A Poisson error distribution was assumed for the number of counted individuals of each fish species as:

$$Y_t \sim \text{Poisson}\left(\exp\left(\log\left(\lambda_t\right) + \alpha X_t + S_t\right)\right) \tag{27.8}$$

where Y_t is the number of counted individuals of each fish species at time t, and α is the coefficient of the effect of habitat condition. The seasonal-adjusted level of the mean proportion of sand at time t (X_t), which was estimated from the SSM as the habitat condition variable, was used, because we preliminarily assumed the increase of sand substrate in the sampling site after deer overabundance upstream, and this study aimed to examine the effects of the long-term trends in that change on fish population dynamics. In this model, the number of counted individuals of each fish species at time t (Y_t) was assumed to be determined by the past state of the fish population ($Y_{t\text{-}1}$) and the present state of habitat characteristics estimated from the SSM (X_t). For missing observation values, a gamma error distribution with a fixed shape parameter (=1) was used as:

$$Y_t \sim \text{Gamma}\left(\exp\left(\log\left(\lambda_t\right) + \alpha X_t + \mathrm{S}_t\right), 1\right) \tag{27.9}$$

because an integer parameter has not been implemented in the statistical framework (Stan Development Team 2017).

Estimation of parameters of the above SSM was conducted by Bayesian framework, and the posterior distribution of parameters was estimated by Markov chain Monte Carlo methods via No-U-Turn sampling (NUTS) in the software STAN ver. 2.17.0 (Stan Development Team 2017), which was called from R version 3.4.1 (R Development Core Team 2017) using the R package “rstan” (Stan Development Team 2017), to obtain posterior distributions for the parameters. The vague prior distribution Normal (0, 100) was used for the directional trend of habitat characteristics, the seasonal adjustment (S), the season-specific increasing rate (r) and density dependence of a given fish population (d), and the coefficient of the effect of habitat condition (α); and half-Cauchy (0, 5) was used for any variance and dispersion parameter terms in the examinations. We used 4 chains, each of which had 10,000 iterations including 5000 burn-in with 2 thinning, resulting in 10,000 values for the posterior distribution of each parameter. Convergence of MCMC computing was checked using the “Rhat” and “n_eff” statistics (Rhat $\leq$1.1 and n_eff $\geq$ 100 for all parameters; Gelman et al. 2013). When the MCMC computing was not convergent, iterations and burn-in were increased up to 40,000 and 20,000, respectively, resulting in 40,000 values in the posterior distribution of each parameter.

27.3 Results and Discussion

27.3.1 Soil and Water Chemistry

Stream nitrate concentrations were lower during the growing season (May–October) than in the dormant season (November–April) in both catchments under base-flow conditions (Fig. 27.3). The mean annual nitrate concentration decreased from 0.30 mg N L^{-1} in 2006 to 0.15 mg N L^{-1} in 2014 in the EC, but was relatively constant, ranging from 0.31 mg N L^{-1} in 2007 to 0.26 mg N L^{-1} in 2014, in the CC (Figs. 27.3 and 27.4). Annual monitoring of riparian understory vegetation in the two catchments indicated that understory cover increased substantially in the EC following the construction of the exclosure, reflecting the recovery of palatable

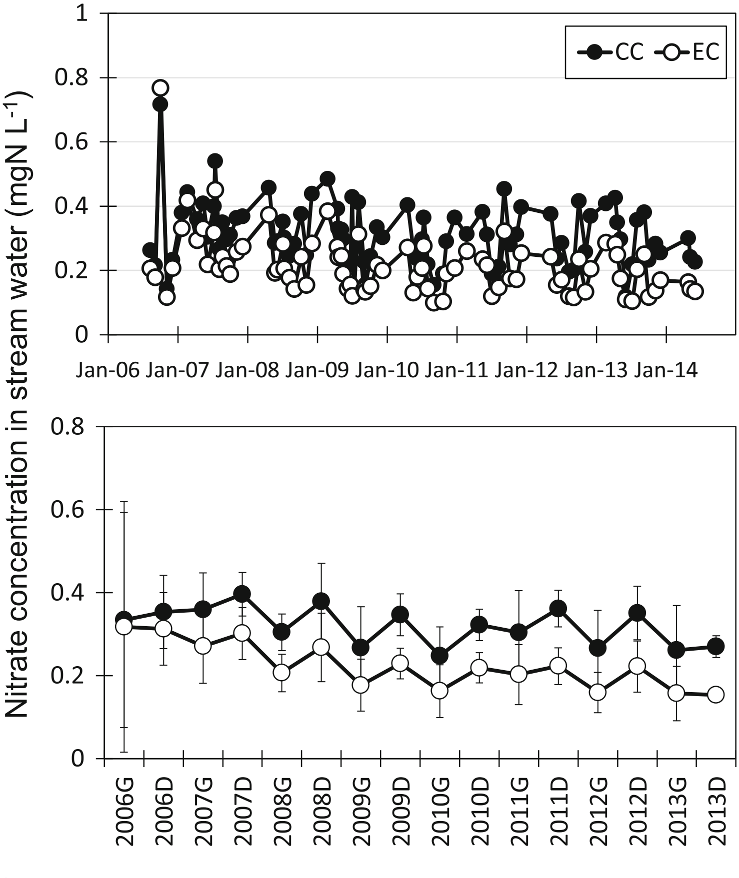

Fig. 27.3 Nitrate concentrations in stream water under base-flow conditions. The upper panel shows nitrate concentrations in each water sample from the EC and CC, and the lower panel shows the periodic average of nitrate concentrations during the growing (G; May–September) and dormant (D; October–April) seasons in each year. Error bars represent standard deviations

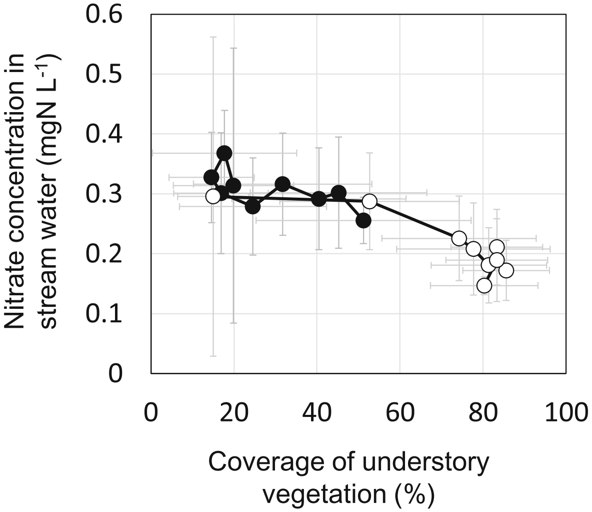

Fig. 27.4 Relationship between understory vegetation cover and mean annual nitrate concentration in streams. Error bars represent standard deviations

herbaceous species in the absence of deer grazing (Fig. 27.2; Sakaguchi, unpublished data). In the CC, understory vegetation cover remained low and stable from 2006 to 2010, after which it slightly increased, possibly due to the increased cover of unpalatable species (Sakaguchi et al. 2012; Sakaguchi unpublished data). There was a significant negative correlation, as determined by Pearson's correlation coefficient, between mean annual nitrate concentration and mean understory vegetation cover (Fig. 27.4; $r = -0.64$, $P < 0.01$ for the CC, $r = -0.85$, $P < 0.01$ for the EC, $r = -0.91$, $P < 0.01$ for all observations). This implies that nitrogen uptake and retention by understory vegetation may at least partly regulate stream nitrate concentrations. The results of soil nitrogen dynamics further supported this finding. At the same slope position, there was no significant difference in the net mineralization rate or the nitrification ratio between the EC and the CC, but soil ammonium and nitrate contents were significantly higher in the CC than in the EC (Fukushima et al. 2014, Table 27.1). This pattern indicates that inorganic nitrogen uptake by vegetation was larger in the EC, which had greater understory vegetation cover. Similar results have been reported from oak stands and open grassland near our study area (Fukushima et al. 2017). Broadly, deer overgrazing may increase nitrate exports from forest soils to streams by retarding nitrogen cycling between understory vegetation and soil.

During the study period, we monitored flow conditions during seven storm events; hydrological conditions during these events are summarized in Table 27.2. Although hydrological conditions in the EC and CC were similar during these events, flow-weighted mean nitrate concentrations were 1.2–1.7 times higher in the CC than in the EC (Table 27.2). In addition, differences in nitrate concentrations between the CC and the EC were most pronounced during events with heavy rain (> 60 mm) relative to lower-precipitation events. This implies that larger amounts of

Table 27.1 Physical and chemical soil parameters along valley and ridge line transects in the exclosure catchment (EC) and the control catchment (CC) (Fukushima et al. 2014)

	Transects in valley lines		Transects in ridge lines	
	EC ($n = 78$)	CC ($n = 103$)	EC ($n = 83$)	CC ($n = 75$)
Soil water content (%)	46.1 (8.20)b	46 (7.99)b	48.7 (5.79)b	52.1 (6.98)a
FH layer thickness (mm)	9.02 (13.10)c	9.33 (15.70)c	43.1 (25.10)a	32.4 (28.10)b
NH_4^+ content (mgN kg dry soil^{-1})	10.6 (5.28)b	10 (4.54)b	10.7 (4.93)b	13.5 (9.04)a
NO_3^- content (mgN kg dry soil^{-1})	5.28 (4.03)bc	7.63 (4.24) a	3.95 (3.18)c	6.41 (3.41)ab
Net N mineralization rate (mgN kg dry soil^{-1} day^{-1})	2.88 (1.66)	2.56 (1.60)	2.95 (1.35)	2.76 (1.28)
Net nitrification rate (mgN kg dry soil^{-1} day^{-1})	2.93 (1.52)a	2.6 (1.57) ab	2.27 (1.39)b	2.03 (0.82)b
C:N ratio	13 (2.05)c	13.1 (1.54) c	17 (2.17)b	18 (2.32)a

Parenthesized values indicate standard deviation. Lowercase letters indicate significant differences among the four transect categories, determined by one-way analyses of variance and Scheffe's *F*-test

soil nitrate may have been leached and transported directly to the stream in the CC, relative to the EC, especially during high-intensity storms.

Flow-weighted mean SS and POM concentrations during storm events were higher in the CC than in the EC for five of the seven events, three of which were accompanied by heavy rain, and there were substantial differences between the two catchments (Table 27.2). Soil surveys indicated that the FH layer on upper slopes was much thinner in the CC than in the EC (Table 27.1). Thus, degradation of the understory due to overgrazing may have led to increased surface soil erosion and a resulting increase in the transport of SSs and POM from forest slopes to streams during storm events.

Annual changes in nitrate concentrations under base-flow conditions and short-term changes in nitrate, SS, and POM concentrations during storm events indicated that deer-induced vegetation degradation led to increased exports from soil to streams. This not only relates to deteriorated soil nutrient status but also negatively affects aquatic ecosystem functioning through eutrophication and/or sedimentation. Although the biomass of understory vegetation was small relative to canopy tree biomass in our study area (0.1–0.2%, Fukushima unpublished data), this ecosystem component plays a key role in retaining soil material and soil nutrients.

Table 27.2 Hydrologic conditions and flow-weighed mean concentrations of nitrate (NO_3^-), suspended sediments (SSs), particulate organic matter (POM), and % OM during seven storm events

		Precipitation (mm)		Stream flow discharge (mm)		Direct runoff ratio (%)		Flow-weighted mean concentration							
								NO_3^- (mg N L^{-1})		SSs (mg L^{-1})		POM (mg L^{-1})		% OM	
No.	Date	Amount	API7	EC	CC	EC	CC	EC	CC	EC	CC	EC	CC	EC	CC
1	2010/9/7	61.5	24.5	13.3	12.3	55	58	0.45	0.77	21.5	37.8	11.8	16.1	55.0	42.6
2	2010/11/22	37.0	76.5	21.3	14.7	34	52	0.28	0.36	1.8	2.8	n.d.	n.d.	n.d.	n.d.
3	2011/6/10	40.5	3.0	12.3	14.7	47	38	0.18	0.25	6.4	4.7	2.2	1.4	34.9	30.2
4	2011/6/24	28.0	9.5	6.2	6.1	75	72	0.18	0.23	6.8	3.7	2.2	1.2	32.8	32.3
5	2011/7/18	314.5	0.0	201.4	226.5	73	72	0.32	0.46	61.9	72.1	16.4	17.8	26.6	24.7
6	2011/8/19	18.0	33.0	4.9	7.7	68	68	0.21	0.25	18.3	25.0	6.6	9.0	35.9	36.1
7	2011/9/1	340.0	7.0	130.2	144.9	65	61	0.37	0.54	95.6	113.3	30.0	33.2	31.4	29.3

API is the sum of precipitation for the 7 days prior to the event. % OM is the percent organic material found in the SSs

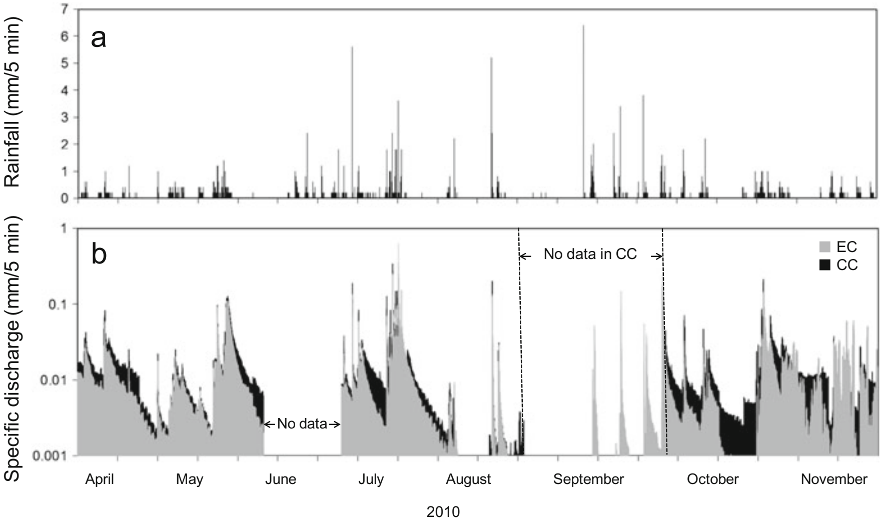

Fig. 27.5 (**a**) Rainfall and (**b**) overland flow component hydrographs (mm/5 min) for the first-order streams in the exclosure catchment (EC) and the control catchment (CC), from Sakai et al. (2013)

27.3.2 *Macroinvertebrates*

Notably, although overland flow inputs to streams increased with higher intensity rainfall in both the EC and the CC, runoff periods lasted longer in the CC following peak rainfall (Fig. 27.5). Overland flow runoff was 1.39 times higher in the CC streams than in the EC streams during the monitoring period. These results imply that deer exclusion decreased overland flow generation via an increase in the cover of understory vegetation and thus mitigated fine-sediment soil runoff to streams.

The proportion of fine-sediment cover in streambeds was greater in the first-order reaches in the CC (mean: 27.9%) relative to the EC (mean: 15.0%) (Sakai et al. 2013). This difference was smaller in the second-order streams (CC, 19.4%; EC, 18.4%) (Sakai et al. 2013). The capacity for sediment transport in river systems is relatively low in headwaters and higher in downstream reaches and then decreases again toward the river mouth (Church 2002); thus, longitudinally changing stream hydraulics may be the cause of this difference, even at the scale of the first- and second-order streams.

The CCA classified macroinvertebrate communities into three groups (Fig. 27.6). Macroinvertebrate communities in the first-order streams in the CC were positively correlated with the proportion of fine sediment and Axis 2, whereas those in the EC showed the opposite pattern. Macroinvertebrate communities in the second-order streams in both the EC and the CC were positively correlated with catchment area, water depth, periphyton biomass, and Axis 1. In the first-order streams in the CC, which had the highest fine-sediment cover, the macroinvertebrate community was characterized by a dominance of a burrower taxon (Ceratopogonidae), which is

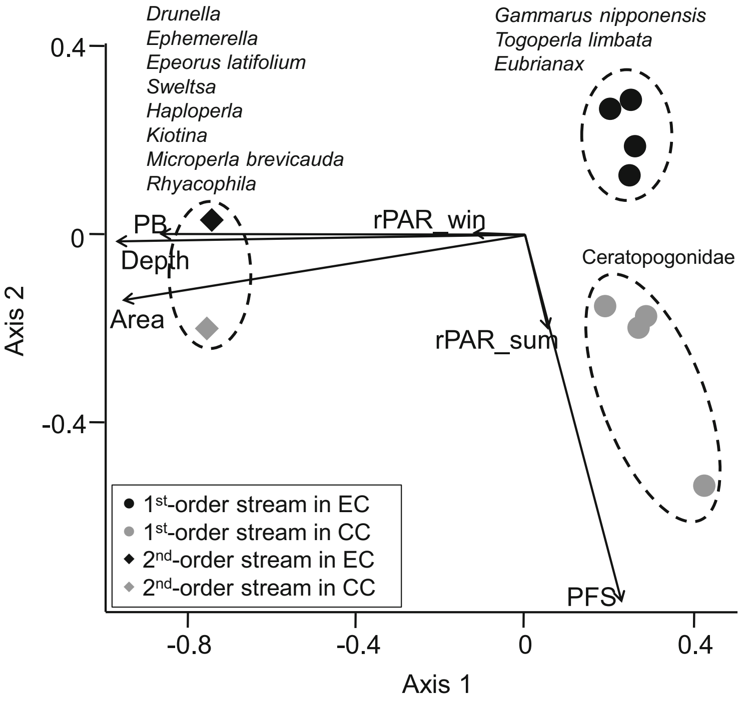

Fig. 27.6 Results of a canonical correspondence analysis based on the abundance of the 50 most abundant taxa and 6 environmental variables (area, catchment area; depth, water depth; PB, periphyton biomass; PFS, % fine sediment on the streambed; rPAR_sum, relative photosynthetically active radiation in August; rPAR_win, relative photosynthetically active radiation in April). Macroinvertebrate communities were classified into three groups, indicated by dashed ovals. Arrows show the strength (length) and direction of the correlations between environmental variables and the ordination axes. Figure taken from Sakai et al. (2013)

typical of fine-sediment habitats, whereas those in the EC were dominated by sprawlers and clingers, which are relatively intolerant to sedimentation (Rabení et al. 2005). These results highlight the indirect effects of deer grazing; exclusion led to a shift in the macroinvertebrate community by mitigating soil runoff. The second-order streams in the EC and the CC were typically dominated by sprawlers, which tend to prefer coarse streambed substrates.

Our findings clearly demonstrate the influence of overgrazing on stream macroinvertebrate communities. Increased soil runoff, which is more pronounced in the first-order streams, relates to a community shift toward fine-sediment-inhabiting burrowers. Introduced fine sediments in the first- and second-order streams may settle out in mild currents in downstream sites, e.g., pools. Therefore, to assess the full scope of indirect effects from deer overgrazing, impacts from headwaters to downstream reaches must be considered.

27.3.3 Fishes

Throughout the study period, the mean proportion of sand increased substantially, while the mean proportion of boulders and the SD of current velocity decreased (Fig. 27.7a–c). These temporal changes support similar observations from other studies of anthropogenic destruction of riparian vegetation (e.g., Roth et al. 1996; Allan et al. 1997). Although our temporal resolution in 2013–2016 was not adequate to determine the exact timing of these shifts, the increase in sand was not apparent prior to 2012. This pattern contrasts with the rapid response to understory vegetation degradation seen in headwater streams. This difference may be due to time lags for

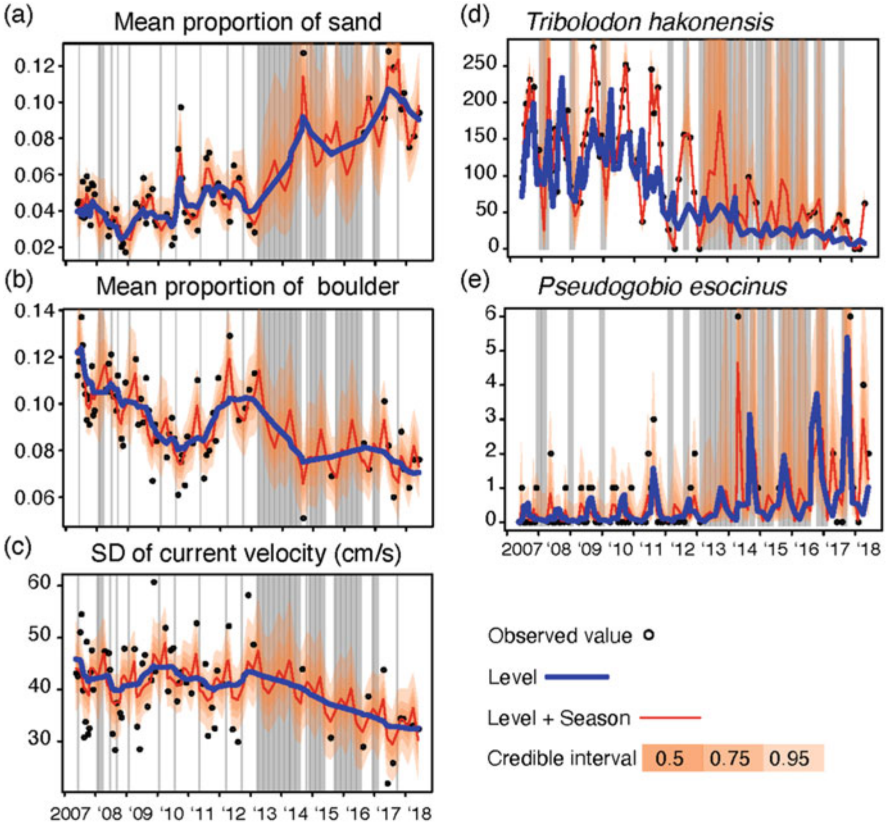

Fig. 27.7 Changes in habitat characteristics;mean proportion of sand (**a**), mean proportion of boulder (**b**), SD of current velocity (**c**), and the number of individuals of *Tribolodon hakonensis* (**d**) and *Pseudogobio esocinus* (**e**) at sampling locations. Estimates and their seasonally adjusted trends were estimated from a state-space model. When observations were incomplete or no observations were available for periods of 2 months or longer, missing values were estimated from posterior distributions of the state of habitat characteristics (shaded areas), from Nakagawa (2019a)

downstream sediment transport, which are dependent on physical distance as well as seasonal and annual variation in water discharge, including flood events (Church 2002; Hamilton 2012).

Among the 13 focal fish species, between 2007 and 2018 we observed a remarkable decrease in *Tribolodon hakonensis* and an increase in *Pseudogobio esocinus* (Fig. 27.7d, e). The results of the SSM indicated a significant negative effect of the change in habitat characteristics on the population dynamics of the former and a significant positive effect on those of the latter (credible interval $\geq 95\%$), but not on that of the other fish species. *T. hakonensis* use pebble-cobble-dominated streambeds with subsurface water upwelling for spawning (Nakamura 1969; Kawanabe and Mizuno 2001) and prefer pool habitats with shelters, such as accumulations of large rocks or deep crevices in bedrock (Katano et al. 2001). Therefore, the decrease in this species may be related to a decrease in its preferred habitat at the study site. By contrast, the benthic-dwelling *P. esocinus* is a vacuum feeder that forages for macroinvertebrates in fine substrates and often buries itself in the sand when threatened (Nakamura 1969; Kawanabe and Mizuno 2001). In 2008, *P. esocinus* primarily inhabited sand-dominated sites downstream of the study site (Nakagawa 2014). The increase in fine sediments in the substrate in the years following may have expanded the distribution of *P. esocinus* within the stream by providing suitable habitat. These findings support the linkage between deer overgrazing in upstream areas and indirect, downstream effects on fish population dynamics.

27.4 Conclusion

Our study demonstrated the effects of deer overgrazing on the substrate and macroinvertebrate and fish community composition in the first- to fourth-order streams via accelerated soil erosion (Fig. 27.8). The magnitude of the indirect impacts varied with stream hydraulics, which determine the particle sizes of deposited sediments; the dominance of animals that prefer fine sediments was detected in the first- and fourth-order streams, but not in the second-order streams. This implies that assessments of deer impacts on stream ecosystems should consider spatial variability in sediment transport and deposition capacities in river networks. Temporally, impacts from deer exclusion on macroinvertebrate community shifts in the first-order streams only became obvious 2–4 years after deer were excluded from the EC (Sakai et al. 2012; Sakai et al. 2013). Therefore, time lags are another critical consideration in ecosystem-management strategies that may be applied to mitigate the impacts of deer grazing on stream ecosystems.

Our findings demonstrate that reduced production and quality of riparian vegetation under overgrazing may alter nutrient cycling between forests and streams. Furthermore, changes in stream-substrate composition indirectly resulting from overgrazing may influence the quality and availability of spawning habitat for fish (Armstrong et al. 2003; Kemp et al. 2011). Although it is unclear whether the elevated nitrate concentrations that we observed were sufficient to affect

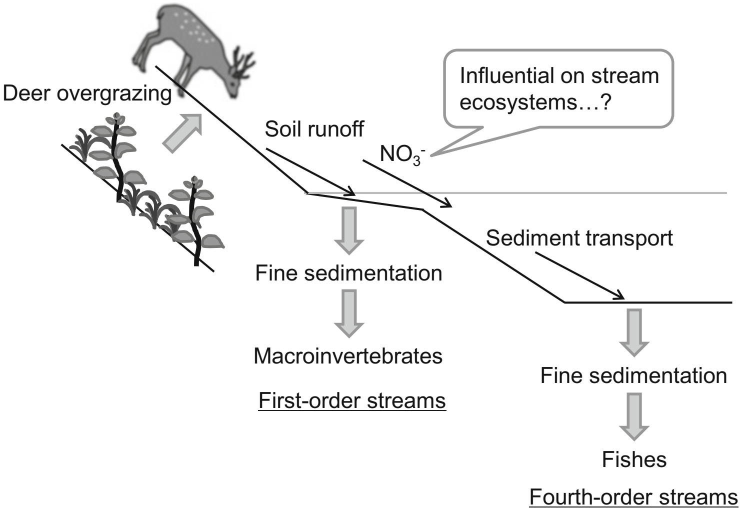

Fig. 27.8 Indirect effects of deer overgrazing on stream ecosystems

macroinvertebrate or fish communities, our findings highlight the linked impacts on terrestrial and aquatic ecosystems of deer overgrazing. Other plot-scale deer-exclusion experiments have examined direct and indirect effects of overgrazing on terrestrial ecosystems and their function; our study demonstrates the importance of catchment-scale studies in linking the abiotic and biotic components of forests and streams. Interdisciplinary assessments that incorporate ecology, hydrology, and fluvial geomorphology may provide effective ecosystem management strategies for mitigating deer overgrazing.

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Part V

Comparison of Life History Characteristics Between Sika Deer and Other Ungulate

Chapter 28
Activity Patterns and Habitat Use Between Sika Deer and Japanese Serow

Takashi Ikeda, Satsuki Nakamori, and Masaki Ando

Abstract Increasing cervid populations can affect other sympatric ungulates. Although sika deer and Japanese serow inhabit Japan, few studies have investigated the activity patterns and habitat use between both ungulates in sympatric areas. Clarifying these trends will provide crucial information for understanding intraspecies relationships, managing both ungulate populations, and conserving their habitats. This chapter aims to clarify the diel activity patterns and habitat use of the two sympatric ungulates. We found no seasonal changes in the diel activity patterns of the ungulates. The sika deer showed crepuscular activity, while the Japanese serow showed cathemeral activity, showing different diel activity patterns between both ungulates. Thus, there is a possibility that the diel activity patterns of both ungulates would overlap at dawn and dusk. A year-round overview of the results from the study in a small-scale river basin shows that sika deer tended to use the western side of the river, and Japanese serow tended to use the eastern side of the river, and this trend is evident in summer. In contrast, both ungulates tended to avoid snow cover in winter and use steeper slopes and ridges in several seasons. These results confirm that there is a partial overlap in spatiotemporal resources in habitat use by sika deer and Japanese serow. Consequently, it is necessary to detect the authentic evidence of the interspecific competition between sika deer and Japanese serow and to understand the changes in this relationship in the current situation where the impact of sika deer is increasing.

T. Ikeda (✉)
Research Center for Wildlife Management, Gifu University, Gifu, Japan
e-mail: ikedat@gifu-u.ac.jp

S. Nakamori
Chubu Branch, Asia Air Survey Co., Ltd, Nagoya, Japan
e-mail: stk.nakamori@ajiko.co.jp

M. Ando
Faculty of Applied Biological Science, Gifu University, Gifu, Japan
e-mail: m_ando@gifu-u.ac.jp

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28.1 Introduction

The growing cervid populations can affect ecosystems directly via effects on foraged plant species and have cascading effects on a wide range of organisms within their habitat via vegetation modification (Rooney and Waller 2003; Côté et al. 2004). Moreover, interspecific competition occurs when multiple species of herbivorous ungulates occur sympatrically and resources are limited (Fraser 1996; Putman 1996; Kalb et al. 2018). Some studies have reported that interspecific competition among herbivorous ungulates negatively affects the populations of disadvantaged species. For example, Corlatti et al. (2019) showed that a recent increase in the population of red deer (*Cervus elaphus*) negatively affected the population growth rate of chamois (*Rupicapra rupicapra rupicapra*).

In the Japanese archipelago, two large herbivorous ungulates, sika deer (*Cervus nippon*) and Japanese serow (*Capricornis crispus*), inhabit Honshu, Sikoku, and Kyushu. The increase in the range and population size of sika deer has influenced natural vegetation and damaged agricultural crops (Ohashi et al. 2014; Ministry of Agriculture, Forestry and Fisheries 2019), and their capture is being promoted to reduce their population (Ministry of the Environment 2016). In contrast, the Japanese serow is an endemic ungulate and is designated as a Special Natural Monument, and serow populations in Kyushu, Shikoku, the Suzuka Mountains, and the Kii Mountains in Honshu are designated as "Threatened Local Populations" in the Red Data Book of Japan (Ministry of the Environment 2020a). Furthermore, the latter two local populations were newly listed in the Red Data Book in 2020, and the impact of vegetation modification of habitats by sika deer has been suspected to be the cause of the decline in the serow population (Ministry of the Environment 2020b). Thus, it is necessary to clarify the relationship between the two ungulates, to implement population management for the sika deer and further establish a conservation scheme for the serows.

Sika deer are gregarious (Maruyama 1981). Radio and GPS telemetry surveys indicate that the northern sika deer populations seasonally migrate to better foraging habitats or less snow cover during the early summer, autumn, and winter (Igota et al. 2004; Izumiyama and Mochizuki 2008; Takii et al. 2012, Chap. 38). Alternatively, Japanese serow is solitary and territorial, maintaining the same territory year-round (Kishimoto and Kawamichi 1996; Ochiai and Susaki 2002; Takada and Minami 2019). In addition, Japanese serow prefers steep slopes and low-visibility shrub thickets, which provide greater security against predators (Takada et al. 2019; Takada 2020). While sika deer have caused serious vegetation decline in natural reserves, including several national parks (Yumoto and Matsuda 2006; Shibata and Hino 2009), Japanese serows cause only minor damage to agricultural and natural vegetation compared to sika deer (Ochiai 2016).

A few studies have investigated sika deer and Japanese serow simultaneously in areas where they inhabit sympatrically. A previous study reported that sika deer might be a habitat generalist and Japanese serow a habitat specialist in terms of vegetation and topography (Takada et al. 2020). Japanese serows tend to use steep terrain and low-visibility sites (Takada et al. 2019; Takada 2020), and sika deer tend to use relatively gentle slopes compared to sympatric Japanese serows (Takada 2020). Fecal composition analyses in some previous studies indicate that sika deer are non-selective grazers that feed on graminoids, especially dwarf bamboo, whereas Japanese serows are selective browsers with a preference for dicots (Takatsuki et al. 2010; Kobayashi and Takatsuki 2012; Endo et al. 2017). However, Takada et al. (2021) showed that they observed food resource partitioning in the montane forest, although both ungulates shared the same abundant food in the alpine grassland, Mt. Asama. These studies indicate that sika deer and Japanese serow can differ in their habitat use and food habits. However, there are some studies on interspecific competition between sympatric sika deer and Japanese serow. In the Ashio Mountains, Tochigi Prefecture, where both ungulates inhabit sympatrically, the number of Japanese serows declined as sika deer increased (Koganezawa 1999), suggesting behavioral interference over habitat between the two ungulates (Nowicki and Koganezawa 2002). These studies also discussed that spatial competition is asymmetrical and disadvantageous only to the Japanese serow.

Understanding the coexistence mechanisms of sympatric wildlife is crucial for the conservation of threatened species (Mueller et al. 2018). In particular, diel activity patterns are one of the key factors in the coexistence mechanism of sympatric wildlife, enabling temporal niche partitioning (Schoener 1974), which is equally important to elucidate interspecific interactions among different sympatric species (Foster et al. 2013; Díaz-Ruiz et al. 2016). Furthermore, a previous study suggested that shifts in community structure (i.e., predator control and the presence of invasive competitors or predators) impacted spatial and temporal niche partitioning of sympatric species exhibiting competitive relationships (Frey et al. 2017). Thus, it would be necessary for wildlife managers to understand diel activity patterns of sympatric species and to gain insight into the mechanisms that promote stable coexistence (Kronfeld-Schor and Dayan 2003). Most studies on the diel activity patterns of sympatric ungulates have used camera traps and have focused on quantitative evaluation (Bhattacharya et al. 2012; Li et al. 2018).

Moreover, the Japanese serow, which has its fixed territories and inhabits solitary, may be negatively affected by the decline in vegetation caused by the increasing sika deer population. However, studies on the differences in diel activity patterns and habitat use between sika deer and Japanese serows are limited in Japan, and the details of interspecies relationships are not evident. Although this chapter provides a limited description of the camera trap survey, we discuss the interspecies relationships, which will contribute to the management of both ungulates and habitat conservation. In this chapter, first, we aim to investigate the seasonal diel activity patterns of the two sympatric ungulates on a large scale (Area 1; Fig. 28.1, Ikeda et al. 2022). Second, we aim to clarify the trends in habitat use by environmental factors of the two sympatric ungulates (Area 2; Fig. 28.1, Nakamori and Ando 2022).

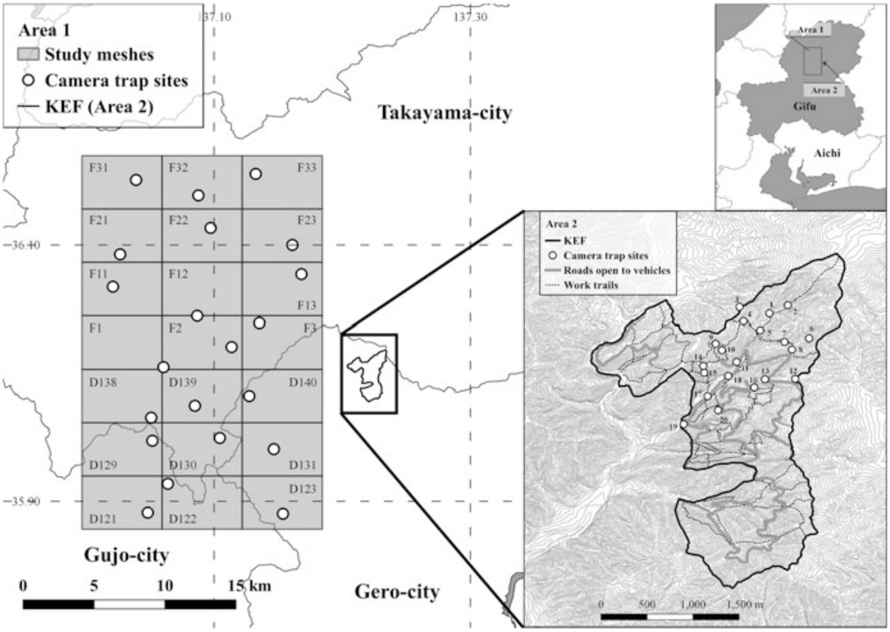

Fig. 28.1 Maps of the northern part of Gifu Prefecture in Central Japan, showing the location of study area 1 and area 2. White circles indicated camera trap sites. We made this map ourselves, using contour lines and roads from the Geospatial Information Authority of Japan

28.2 Materials and Methods

28.2.1 Study Area

To investigate diel activity patterns, we conducted this study in the northern part (35°52′ N–36°10′ N, 137°00′ E–137°11′ E) of Gifu Prefecture in Central Japan, where we included 21 study meshes of 5.5 × 4.6 km (525 km^2; Fig. 28.1). We collected meteorological data in 2018 from the Takayama weather station (36°09′ N, 137°15′ E, 560 m) located in the northern part of the study area. The maximum temperature and minimum temperature in each season are 13.4 and −6.5 °C in winter, 26.9 and 5.5 °C in spring, 32.8 and 16.2 °C in summer, and 20.4 and −0.4 °C in autumn, respectively. In Area 1, the vegetation mainly included deciduous broad-leaved trees (47.2%) and evergreen conifers (36.0%). The majority of canopy species for the former vegetation type are Japanese oak (*Quercus crispula*), jolcham oak (*Quercus serrata*), and Japanese chestnut (*Castanea crenata*), while the majority of canopy species for the latter vegetation type are Japanese cypress (*Chamaecyparis obtusa*), Japanese cedar (*Cryptomeria japonica*), and sawara cypress (*Chamaecyparis pisifera*).

Habitat use was investigated at the Kuraiyama Experimental Forest (KEF) of Gifu University, located in Gero City, Gifu Prefecture, Central Japan (553 ha, 35°97 N, 137° 02 E). The meteorological data were similar to those from the Takayama weather station. The altitude of the study area ranges from 830 to 1210 m; the Shinnomata Valley extending from the northeast to the southwest in the center of the survey area forms a small-scale river basin. The eastern side of the valley is dominated by the northwestern slope, and the western side is dominated by the southeastern slope (Fig. 28.1). This site consists of a variety of forest types, including natural broad-leaved forests dominated by Japanese beech (*Fagus crenata*), jolcham oak, Japanese oak, natural coniferous forests dominated by Japanese cypress and Asunaro (*Thujopsis dolabrata*), and coniferous plantations of Japanese cedar, cypress, and larch (*Larix kaempferi*). The understory vegetation is dominated by dwarf bamboo (*Sasa senanensis*). A substantial disappearance of understory vegetation has not yet been identified, although partial declines in dwarf bamboo cover and coniferous shrub tree (*Cephalotaxus harringtonia* var. *nana*) communities have been observed during field observations. The increase and expansion of sika deer have become problems in Gifu Prefecture (2016). Tsunoda et al. (2017) also demonstrated the consequent decline of shrub layer vegetation in Gifu Prefecture, using the shrub layer decline rank (Fujiki et al. 2010).

28.2.2 Diel Activity Pattern

Between August 2017 and November 2019, we strapped 21 passive infrared triggered camera traps (HykeCam SP2, Hyke Co. Ltd., Asahikawa, Japan) to trees (approximately 1 m above the ground) at the survey sites. These cameras were set at animal trails and dirt roads, where animal signs (e.g., scars and dung) were evident. Three photographs were taken per trigger with 5 min of hibernation between consecutive events. We excluded several photos of the same ungulates within 30 min, following Ohashi et al. (2013). Not all cameras could be operated during the study period as there were several technical difficulties (i.e., camera thefts and malfunctions) during their installation. We defined four seasons: winter (January–March), spring (April–June), summer (July–September), and autumn (October–December). Considering daily sunrise and sunset time, we also classified the photos of both ungulates into three time periods: daytime (from 1 h after sunrise to 1 h before sunset), nighttime (from 1 h after sunset to 1 h before sunrise), and twilight (1 h before and after sunrise and sunset). Thereafter, the total number of these ungulates photographed in each hour and time period was determined. We did not provide diel activity patterns in winter because of the low number of Japanese serows photographed by each camera and the technical problems of using cameras during this season.

28.2.3 Habitat Use

To assess the environmental factors affecting the habitat use of sika deer and Japanese serow, we installed passive infrared triggered camera traps (Ltl Acorn 5210a, OLDBOYS OUTDOORS, USA) at 20 sites in KEF on November 22, 2013. The camera trap sites were located along human/animal trails: at the valley bottom ($n = 7$), east side ($n = 7$), and west side ($n = 6$) (Fig. 28.1). Three photographs were taken per trigger with 1 min of hibernation between consecutive events. In May 2015, all camera traps were replaced with another model (HykeCam SP108-J, Hyke Co. Ltd., Asahikawa, Japan). In this study, data from December 1, 2013, to November 30, 2016 (3 years; 1096 days) were used for the analyses. The frequency of each ungulate photographed at each site was used as a proxy for habitat use frequency.

At each camera trap site, we recorded the following environmental factors: the coverage of dwarf bamboo (% cover in ca. 1 ha around camera traps), forest type (broad-leaved, coniferous, and mixed forests), slope (mean degree around camera trap), topography (ridges, valleys, and hillsides), snow depth (average of five measurements taken in late February 2014–2017), elevation, and location in KEF (east side, west side, and bottom of Shinnomata Valley).

28.2.4 Data Analysis

28.2.4.1 Temporal Patterns

First, we examined the relationship between the hours of the day and the number of photos of two sympatric ungulates and assessed their diel activity patterns. In this study, it was difficult to adopt a circular package (Lund and Agostinelli 2017) and an overlap package (Meredith and Ridout 2020) because these packages provide diel activity patterns throughout the study area without considering the distance between camera sites (the average distances among camera sites: 4.1–7.4 km). Thus, if the distance between cameras is large, each camera's records should be regarded as an independent variable. Therefore, we clarified diel activity patterns while considering the differences in each camera, using a generalized additive mixed model with a Poisson distribution in the mgcv package (Wood 2019). The total number of ungulates photographed for each hour and camera was set as the response variables, and the hours were set as explanatory variables. Furthermore, we set each camera as a random effect and trap days as an offset term for each camera.

Thereafter, we analyzed the differences in the activity of two sympatric ungulates during specific time periods (daytime, nighttime, and twilight). We tested whether the photographic frequency (the number of ungulates photographed per hour) differed among these time periods, using a generalized linear mixed model (GLMM) with a negative binomial distribution in the lme4 package (Bates et al.

2015) and the multcomp package (Hothorn et al. 2019). The total number of ungulates photographed for each day, camera, and time period were set as the response variables, and three time periods were set as explanatory variables. Additionally, we set each camera as a random effect and the length of each time period (h) as an offset term. Thereafter, we used Tukey's HSD multiple comparison test and tested the differences in photographic frequency among the three time periods.

All statistical analyses were performed using R version 3.4.0.

28.2.4.2 Trends in Habitat Use

To analyze the trends in habitat use by environmental factors of sika deer and Japanese serow, GLMM was used. In this analysis, we defined winter as the period when there is mainly snow cover because some previous studies have pointed out that snow cover affects food availability for both sika deer and Japanese serow (Seto et al. 2015; Takatsuki et al. 1995). In this study, we categorized the four seasons as follows: spring (March to May), summer (June to August), autumn (September to November), and winter (December to February). Models were constructed for each ungulate during each season. The frequency of camera traps triggered by sika deer and Japanese serow was set as a response variable, and the coverage of dwarf bamboo, forest type, slope, topography, snow depth (winter models only), elevation, and location in KEF were set as explanatory variables. Each camera site was set as a random effect. In all models, the error distribution of response variables was set as a Poisson distribution with a logarithmic link function, and the operating days of the camera traps at each site were set as the offset term. Each forest type was estimated as a fixed term, with broad-leaved forests set at zero. Similarly, topography was estimated, with the hillside set as zero, and the location in KEF was estimated, with the eastern side set as zero.

All possible model structures, with the response and explanatory variables, were calculated. The total number of built models was 64 in spring, summer, and autumn for each ungulate and 128 in winter. All models were ranked according to their AIC values in ascending order. Differences in AIC values between each model and the model with the minimum AIC were calculated as the Delta-AIC in each model. Delta-AIC values <2 indicate an approximately equal fit of the models (Burnham and Anderson 2002). Thus, models with a Delta-AIC <2 were selected as the best model group. In this study, we selected the best model from the best model group with the following three steps: (1) select the model(s) with the fewest non-significant explanatory variables in the model, (2) select the model(s) with the fewest explanatory variables consisting of the model, and (3) select the model with the lowest AIC as the best model. R and lme4 packages (Bates et al. 2015) were used for all analyses.

28.3 Results

28.3.1 Diel Activity Pattern

From 11,896 camera trap days between August 2017 and November 2019, we recorded 3,888 deer in 3,368 photo events and 909 serows in 859 events. Of these photographs, we used a total of 3,714 for our analysis. We found significant relationships between the hours of the day and the number of animals photographed for both ungulates, excluding Japanese serow in autumn (Table 28.1). Sika deer had clear activity peaks before sunset and after sunrise in spring and summer (i.e., 18:00 and 6:00) and after sunset and before sunrise in autumn (i.e., 17:00 and 5:00) (Fig. 28.2). Japanese serows seemed to be active after midnight in spring and around midnight and noon in summer (Fig. 28.2).

Throughout the study period, the photographic frequency of sika deer during twilight was significantly higher than during other time periods, while there were no significant differences in the frequencies between daytime and nighttime (Fig. 28.3, Table 28.2). Although Japanese serows seemed to show cathemeral activity, there were no significant differences in the frequencies among the three time periods, except in summer (Fig. 28.3, Table 28.2).

28.3.2 Habitat Use

The environmental factors of the camera trap sites are diverse. The snow depth (mean ± SD) in KEF was 66 ± 20, 132 ± 27, and 4 ± 8 cm in the month of February for the respective years of 2014, 2015, and 2016.

The total number of camera triggers was 39,960. Both the ungulates were photographed at all sites. The number of camera triggers caused by sika deer ($n = 6481$) was larger than that caused by the Japanese serow ($n = 1602$).

The trends in habitat use of both ungulates are summarized in Tables 28.3 and 28.4. In several environmental factors, the trends of the two ungulates were similar to

Table 28.1 Results of a generalized additive mixed model with a Poisson distribution for the relationship between hours of the day and the number of two sympatric ungulates photographed

Season	edf	*F*	*p*
Sika deer			
Spring	6.279	8.968	***
Summer	7.528	14.760	***
Autumn	7.939	10.150	***
Japanese serow			
Spring	2.576	6.597	**
Summer	3.941	3.263	**
Autumn	1.000	0.430	*N.S.*

Cited from Table 2 of Ikeda et al. (2022)

edf estimated degrees of freedom

***$p < 0.001$, **$p < 0.01$, *N.S.*: $p \geq 0.05$

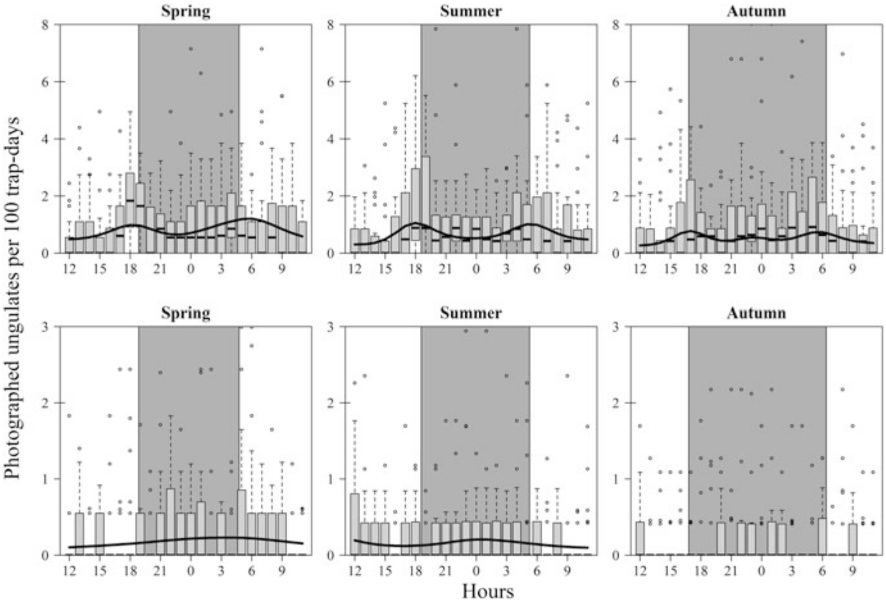

Fig. 28.2 Seasonal diel activity patterns of sika deer (upper) and Japanese serows (lower) using the results of a generalized additive mixed model from spring to autumn. The solid line represents the mean trend, as fitted by this model. Gray- and white-shaded areas indicate night (from seasonal medians of sunset to seasonal medians of sunrise) and day (from seasonal medians of sunrise to seasonal medians of sunset), respectively. (Cited from Fig. 3 and Fig.4 of Ikeda et al. (2022))

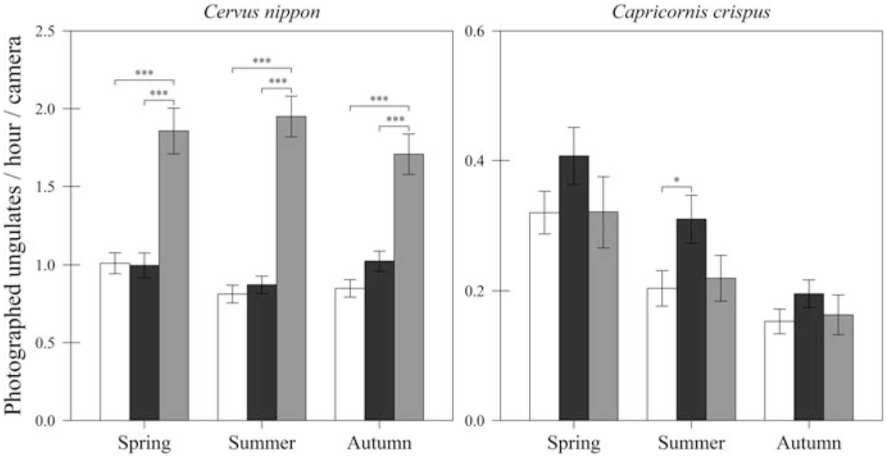

Fig. 28.3 Average daily photographic frequencies (number of animals photographed per hour per camera) of sika deer (upper) and Japanese serows (lower) and SE from spring to autumn. White-, black-, and gray-shaded areas indicate daytime (from 1 h after sunrise to 1 h before sunset), nighttime (from 1 h after sunset to 1 h before sunrise), and twilight (1 h before and after sunrise and sunset), respectively. (Cited from Fig. 6 of Ikeda et al. (2022))

Table 28.2 Results of the multiple comparison test for differences in the photographic frequency among three time periods

Season	Variables	Estimate	SE	*Z*	*p*
Sika deer					
Spring	Nighttime vs. daytime	0.025	0.098	0.252	*N.S.*
	Twilight vs. daytime	0.640	0.098	6.499	***
	Twilight vs. nighttime	0.615	0.106	5.832	***
Summer	Nighttime vs. daytime	0.183	0.088	2.086	*N.S.*
	Twilight vs. daytime	0.933	0.087	10.745	***
	Twilight vs. nighttime	0.750	0.090	8.363	***
Autumn	Nighttime vs. daytime	0.167	0.089	1.888	*N.S.*
	Twilight vs. daytime	0.598	0.096	6.243	***
	Twilight vs. nighttime	0.431	0.090	4.808	***
Japanese serow					
Spring	Nighttime vs. daytime	0.259	0.145	1.790	*N.S.*
	Twilight vs. daytime	−0.016	0.193	−0.085	*N.S.*
	Twilight vs. nighttime	−0.275	0.196	−1.401	*N.S.*
Summer	Nighttime vs. daytime	0.375	0.146	2.564	*
	Twilight vs. daytime	0.086	0.196	0.440	*N.S.*
	Twilight vs. nighttime	−0.288	0.194	−1.487	*N.S.*
Autumn	Nighttime vs. daytime	0.262	0.168	1.565	*N.S.*
	Twilight vs. daytime	0.102	0.227	0.448	*N.S.*
	Twilight vs. nighttime	−0.161	0.210	−0.765	*N.S.*

Cited from Table 3 of Ikeda et al. (2022)
***$p < 0.001$, *$p < 0.05$, *N.S.*: $p \geq 0.05$

each other. The snow cover in winter was negative for both ungulates. In addition, Japanese serows frequently used steeper slopes and ridges in all seasons, while sika deer also preferred steeper slopes and ridges in autumn and winter. However, other factors had different effects on habitat use in each ungulate. In summer and winter, sika deer were frequent in the west side of KEF, while Japanese serows were frequent in the eastern side. Sika deer frequently used broad-leaved forests in autumn, while Japanese serows frequently used mixed forests in spring and coniferous forests in winter. Sika deer were found in higher elevations in spring, whereas Japanese serows were found in lower elevations in spring, summer, and autumn.

28.4 Discussion

28.4.1 Diel Activity Pattern

Sika deer and Japanese serows, sympatric ungulates, were found to have different seasonal diel activity patterns. We found no seasonal changes in the diel activity patterns of sika deer, showing crepuscular activity. In contrast, the seasonal diel

Table 28.3 Estimated coefficients of variables adopted in the best model in each season by GLMM analysis for habitat use of sika deer

Season	Variables	Estimate	SE	*Z*	*p*
Spring	Elevation	0.506×10^{-2}	0.218×10^{-2}	2.323	*
Summer	Location in KEF: valley's bottom	−0.604	0.408	−1.481	*N.S.*
	Location in KEF: western side	1.030	0.417	2.469	*
Autumn	Forest type: coniferous	−0.837	0.387	−2.166	*
	Forest type: mixed	0.311×10^{-1}	0.404	0.770×10^{-1}	*N.S.*
	Slope	0.637×10^{-1}	0.241×10^{-1}	2.639	**
	Topography: ridge	0.925	0.427	2.165	*
	Topography: valley	0.500	0.379	1.319	*N.S.*
Winter	Slope	0.896×10^{-1}	0.247×10^{-1}	3.621	***
	Topography: ridge	1.610	0.510	3.156	**
	Topography: valley	1.381	0.488	2.831	**
	Snow depth	-0.274×10^{-1}	0.114×10^{-2}	2.410×10	***
	Location in KEF: valley's bottom	1.398	0.461	3.033	**
	Location in KEF: western side	1.854	0.418	4.435	***

Modified from Table 2 of Nakamori and Ando (2022)
***$p < 0.001$, **$p < 0.01$, *$p < 0.05$, *N.S.*: $p \geq 0.05$
In categorical variables, the coefficients, broad-leaved (forest type), hillside (topography), and east side (location in KEF) are set as zero

activity pattern of Japanese serows, which inhabit the sika deer sympatrically, mainly showed cathemeral activity throughout the study period.

In general, previous studies have reported that sika deer showed crepuscular activity (Ikeda et al. 2015, 2016). However, other studies have suggested that deer have shifted their diurnal activity to nocturnal activity and mainly showed nocturnal activity at high levels of human disturbance (van Doormaal et al. 2015; Ikeda et al. 2019). Thus, there was almost no human disturbance on sika deer in this study area, and there were no seasonal changes in activity patterns of sika deer from spring to autumn, which is consistent with the observations from a previous study in Hokkaido (Ikeda et al. 2016).

Few studies using camera traps have reported diel activity patterns of Japanese serows at the population level. At the individual level, Japanese serows showed cathemeral activity based on the results from a telemetry survey (Ochiai 2016). Previous studies have reported that Himalayan serows are active from 06:00 to 08:00 and from 16:00 to 22:00 (Bhattacharya et al. 2012), while mainland serows (*Capricornis sumatraensis*) show nocturnal activity in summer and winter (Liu et al. 2013), and Chinese serow (*Capricornis milneedwardsii*) have activity peaks at dawn (07:00–08:00) and dusk (17:00–18:00) (Li et al. 2018). As with the results at

Table 28.4 Estimated coefficients of variables adopted in the best model in each season by GLMM analysis for habitat use of Japanese serow

Season	Variables	Estimate	SE	*Z*	*p*
Spring	Forest type: coniferous	0.292	0.249	1.173	*N.S.*
	Forest type: mixed	0.860	0.284	3.024	**
	Slope	0.496×10^{-1}	0.143×10^{-1}	3.455	***
	Topography: ridge	1.098	0.262	4.184	***
	Topography: valley	0.648	0.305	2.124	*
	Elevation	-0.595×10^{-2}	0.101×10^{-2}	−5.891	***
	Location in KEF: valley's bottom	−1.438	0.333	−4.319	***
	Location in KEF: western side	−0.469	0.245	−1.912	*N.S.*
Summer	Slope	0.521×10^{-1}	0.218×10^{-1}	2.393	*
	Topography: ridge	0.974	0.321	3.032	**
	Topography: valley	0.348×10^{-1}	0.338	0.103	*N.S.*
	Elevation	-0.378×10^{-2}	0.170×10^{-2}	−2.231	*
	Location in KEF: valley's bottom	−0.713	0.436	−1.636	*N.S.*
	Location in KEF: western side	−1.221	0.297	−4.112	***
Autumn	Slope	0.418×10^{-1}	0.140×10^{-1}	2.986	**
	Topography: ridge	0.893	0.276	3.239	**
	Topography: valley	0.362	0.277	1.305	*N.S.*
	Elevation	-0.269×10^{-2}	-0.927×10^{-3}	−2.902	**
	Location in KEF: valley's bottom	−0.893	0.285	−3.131	**
	Location in KEF: western side	−1.016	0.243	−4.173	***
Winter	Forest type: coniferous	1.252	0.403	3.109	**
	Forest type: mixed	0.637	0.449	1.420	*N.S.*
	Slope	0.613×10^{-1}	0.239×10^{-1}	2.571	*
	Topography: ridge	1.019	0.318	3.208	**
	Topography: valley	0.781×10^{-1}	0.383	0.204	*N.S.*
	Snow depth	-0.163×10^{-1}	0.266×10^{-2}	−6.134	***

Modified from Table 3 of Nakamori and Ando (2022)

***$p < 0.001$, **$p < 0.01$, *$p < 0.05$, *N.S.*: $p \geq 0.05$

In categorical variables, the coefficients, broad-leaved (forest type), hillside (topography), and eastern side (location in KEF) are set as zero

the individual level, the Japanese serows in this study area showed cathemeral activity, because sika deer were more active during the twilight time period, unlike

Japanese serows, and they showed different diel activity patterns than those of sika deer.

In Japan, most studies on interspecific competition between deer and Japanese serows have been reported in addition to other diel activity patterns. Some studies have reported that the diet and habitat of both ungulates are different (Endo et al. 2017; Takada et al. 2020), while another study indicated that there was a dietary overlap but a spatial gap between these ungulates (Yamashiro et al. 2019). Similarly, we suggest that the Japanese serows in this study showed different diel activity patterns for sika deer. These differences could be attributed to several factors. First, Nowicki and Koganezawa (2002) indicated that the response of Japanese serows to sika deer is more pronounced than that of sika deer, suggesting that Japanese serows avoid sika deer. Second, another study showed that the food habits of both ungulates were influenced by the amount of food resources, and both ungulates had different food habits in habitats with diverse food resources (Takada et al. 2021). Similarly, we suggest that the Japanese serows in the current study showed different diel activity patterns of sika deer. Therefore, these factors may be related to temporal differences between the ungulates.

Several studies have indicated that the population density of Japanese serows decreased due to the high deer density (Koganezawa 1999; Nowicki and Koganezawa 2002; Hashimoto and Mori 2018), and there is a possibility that the interspecific competition between both ungulates affects the survival of the Japanese serows. Accordingly, a previous study suggested that it would be useful to monitor competitive interactions between sika deer and Japanese serows in areas with increasing deer population densities (Kobayashi and Takatsuki 2012). Another study in Gifu Prefecture evaluated the impact of sika deer browsing on shrub-layer vegetation using the shrub-layer decline rank (Tsunoda et al. 2017). Systematic camera trap surveys have been initiated throughout Gifu Prefecture since July 2021. Therefore, further studies are needed to elucidate the impact of sika deer on the ecology (i.e., distribution, food habits, and diel activity pattern) of Japanese serows, considering the density and distribution of both ungulates at a large-scale level.

28.4.2 Habitat Use

From the results of the KEF survey, it was found that some factors affecting habitat use were similar (snow depth, slope, and ridge), while others were found to be different (location in KEF, elevation, and forest type) for both ungulates.

The coefficients of snow depth in both ungulates were estimated to be negative, indicating that both ungulates avoided snow in winter. Sakuragi et al. (2003) reported that sika deer migrate to areas with less snow cover during winter. Seto et al. (2015) suggested that deep snow prevented sika deer access to understory vegetation, which is their major food resource. Takatsuki et al. (1995) also suggested that snow cover reduces forage availability for Japanese serows. Therefore, our results could also be derived from the decline in food availability due to snow cover.

Some studies have indicated that Japanese serows tend to occupy steep terrain and low-visibility sites related to predation risk (Takada et al. 2019; Takada 2020). As for sika deer, Takii et al. (2012) described that sika deer tend to occupy regions with steeper slopes in winter to avoid hunting disturbances. Our results showed that Japanese serows in the KEF frequently use steeper slopes in all seasons. Moreover, they also showed that sika deer in the KEF frequently used steeper slopes in autumn and winter. In Gifu Prefecture, the hunting season (usually in winter) starts on November 1 in recent years, and in our study, November is included in autumn. Even though hunting was inhibited in KEF, the surrounding forests were allowed for hunting. Therefore, the trend of using steeper slopes in both ungulates may also be a response to avoid predation/hunting risk. However, the reason for the frequent use of the ridge by both ungulates is still unknown.

About the location in KEF, the eastern side of the valley mainly consists of northwestern facing slopes (Fig. 28.1), and snow would not melt easily due to the short daylight on the slope. Therefore, obtaining food in winter may be more difficult compared to the western side of the valley. Because sika deer prefer certain suitable environments depending on the season (Izumiyama and Mochizuki 2008), their presence in the eastern regions of the valley may be limited because of the low food availability in winter. In contrast, the presence of Japanese serows on the eastern side of the valley in summer and autumn and lower-elevation areas in all seasons except winter is still unclear. However, during winter, the two ungulates may have avoided the eastern side in winter because of the snow cover. In addition, there is a difference in the trend of elevation, but the reason for this is still unknown.

Previous studies have shown that habitat use by sika deer is affected by understory and forest vegetation (Sakuragi et al. 2003; Ito and Takatsuki 2009). Another study showed that sika deer in Yamaguchi Prefecture foraged heavily on the acorns of Japanese Chinquapin (*Castanopsis sieboldii*), sawtooth oak (*Quercus acutissima*), and jolcham oak in November (Weerasinghe and Takatsuki 1999). Our results showed that sika deer used broad-leaved and mixed forests than coniferous forests in autumn (Table 28.3). Compared with the surrounding forests dominated by coniferous plantations, KEF contains deciduous broad-leaved forests with many acorn trees (i.e., Japanese beech, jolcham oak, and Japanese oak). This trend suggests that sika deer may frequently use broad-leaved and mixed forests, where the availability of acorns is high in autumn. As for Japanese serows, our results showed that Japanese serows used coniferous forests in winter and mixed forests in spring (Table 28.4). Some previous studies on fecal pellet surveys have pointed out that Japanese serows often use coniferous forests as defecation sites (Haneda et al. 1966; Miyazawa et al. 2005). Previous studies on radiotelemetry tracking have pointed out that Japanese serows often use coniferous forests in winter (Okumura 1989; Tano et al. 1994; Otsuki and Ito 1996). The trend of winter habitat use by Japanese serows in this study was consistent with that from previous studies.

As mentioned in Sect. 28.1, the decline in understory vegetation by sika deer is currently a major problem in Japan. Moreover, Japanese serows are expected to be affected by competition with sika deer for food resources and habitat use. In KEF, the disappearance of *Cephalotaxus harringtonia* var. *nana* community and the partial decline in dwarf bamboo reflect the impact of sika deer on understory vegetation. The vegetation degradation by sika deer is an ongoing problem that will not be resolved in the near future. As the effects of deer increase in the KEF, the interspecific relationship, that is, the degree of interference competition between the two ungulates, is expected to change gradually. Monitoring this change will enable the detection of interspecific competition between the ungulates and evaluate their further impact. For this purpose, it is important to conduct long-term monitoring such as camera trap surveys and observation of vegetation changes in anticipation of successive changes in the impact of deer.

28.5 Conclusion

In this study, we investigated the activity patterns and habitat use of sika deer and Japanese serows. The activity pattern and habitat use trends varied spatiotemporally for the two ungulates; seasonal changes in these trends were evident from the study. Therefore, if there is an interspecific competition between the two ungulates, the intensity may change over time and space. However, the results of this study indicate that the current status of activity patterns and habitat use of both ungulates is insufficient to indicate interspecific interactions and their intensity. Although studies have reported the interspecific competition between the two ungulates (Nowicki and Koganezawa 2002; Takada et al. 2020, 2021), further studies with sufficient data and appropriate analyses should be conducted for sika deer management and Japanese serow conservation in the future.

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Chapter 29
Sika in the British Isles: Population Ecology, Spread and Impacts of an Introduced Species

Rory Putman and Josephine Pemberton

Abstract Since their introduction to the British Isles approximately 150 years ago, sika deer have expanded their distributional range and established many large free-ranging populations in Scotland, England (Great Britain) and in Ireland. As such, they have become a significant resource, or pest, depending on various local, regional or national objectives. Genetic analysis has proven that several populations are hybridized to some degree with red deer (*Cervus elaphus*) and that there may be few populations extant of pure Japanese sika. Throughout this chapter therefore the term sika is used to describe sika and sika-like hybrids, on the basis that we use this term to refer only to phenotypic character, with no presumption of underlying genetic make-up. In England, populations currently remain local and comparatively isolated, although they are spreading across the south and southwest of the country. The largest populations of sika within Great Britain are currently found in Scotland, partly due to the number and extent of introductions (Ratcliffe, Mammal Rev 17:39–58, 1987) but also because of the widespread availability of suitable habitat. Populations in Scotland have shown significant increase in number and steady expansion in distribution. Culls of sika have increased steadily, but there is little sign that they have affected their abundance or distribution. Sika appear to reach higher densities in suitable habitat than other species and at high densities can impose significant impacts on commercial forestry and vulnerable natural habitats such as wetlands. Throughout their range, management has therefore been focused on controlling impacts on forestry and conservation habitats and containing rates of expansion and hybridization. In this chapter we review the general ecology of sika deer in the British Isles (habitat use, feeding ecology, population ecology), the impacts of sika deer on habitats, the impacts on native deer species through competition and hybridization and the management approaches applied.

Note: this chapter is offered as an update to Swanson and Putman (2009).

R. Putman (✉)
Institute of Biodiversity, Animal Health and Comparative Medicine, University of Glasgow, Glasgow, UK
e-mail: putman.rory@gmail.com

J. Pemberton
Institute of Evolutionary Biology, University of Edinburgh, Edinburgh, UK
e-mail: J.Pemberton@ed.ac.uk

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29.1 History

Sika deer were first brought to the British Isles in 1860 when a pair of Japanese and a pair of Manchurian sika were presented to London Zoo (Whitehead 1964). Later that year, six Japanese deer were delivered to Viscount Powerscourt for his deer park at Enniskerry in Ireland (Powerscourt 1884). These animals were subsequently bred and distributed, either directly or indirectly, to enclosed deer parks throughout Ireland, Scotland and England and were commonly kept alongside many other deer species (Ratcliffe 1987). Only two introductions are documented to have come directly from Japan: one to Dawyck in the Scottish Borders (southern Scotland near the border with England) and the other (now possibly extinct) to Pixton in Devon, England (Ratcliffe 1987). However, the origins of some introductions are not recorded, for example, those of the extensive population in the Poole Basin in Dorset and those in the New Forest in Hampshire. Subsequent genetic analysis (Diaz et al. 2006) indicates that the Dorset sika are hybrid in nature, but some doubt remains about the extent of hybridization among the New Forest population. Most of the introduced deer remained fenced within park boundaries until around 1910–1920, at which point they were either deliberately released or escaped to form feral populations of varying success.

The origin and subspecific status of the sika stocks introduced to the British Isles has generated much interest because of the possible role it may have played in the hybridization of sika with red deer (Lowe and Gardiner 1975; Harrington 1982; Ratcliffe 1987; Ratcliffe et al. 1992; Abernethy 1994). Most populations are thought to have originated directly or indirectly (via Powerscourt) from the southern Japanese archipelago and belong to the subspecies *C. n. nippon* (Ratcliffe 1987; Abernethy 1994). However, mainland Chinese (*C. n. hortulorum*) and Taiwanese (Formosan) (*C. n. taiouanus*) sika stocks were known to have been kept at the same time in some park collections, and it is possible that these may have contributed genetically to various park and feral populations (Whitehead 1964; Ratcliffe et al. 1992).

Although there are some differences in appearance between British sika populations (e.g. coat colour and skull shape), genetic analysis of several populations (including Argyll, Dorset, Fife and Scottish Borders) indicates that all are essentially of Japanese origin (*C. n. nippon*) and, interestingly, have all originated from the same area around Nagasaki on Kyushu Island, Japan (Swanson 1999; Goodman et al. 2001; Diaz et al. 2006). The molecular markers found in both the Wicklow and Killarney populations in Ireland also show a similar pattern to those found elsewhere in Scotland and England (G. Swanson, unpublished data).

29.2 Current Distribution

Following their introduction to deer parks and private collections between 1870 and 1930, sika deer subsequently escaped or were released into the surrounding habitat (Whitehead 1964; Ratcliffe 1987).

In Ireland, sika deer occur in the wild in both the northern and southern parts of the island, with major populations in the south in Killarney, centred on the National Park, in Donegal, and around the mountains of Wicklow. In Northern Ireland, there are significant populations associated with the old deer park of Colebrooke in County Fermanagh, and others in County Limerick and County Tyrone, probably continuous with populations in Donegal. Smaller populations were established as escapees from deer parks in County Monaghan, and County Down, but the current status of these is unknown.

In Scotland, sika are now widely distributed on the mainland with some 14,000 km^2 colonized by the species (Putman 2008). The main centres of population are in Peeblesshire, Argyll, Inverness-shire, Ross and Cromarty and Sutherland; all show dramatic recent expansion in range (Ward 2005; Ward et al. 2008). Despite their widespread introduction to numerous deer parks in the nineteenth century, sika deer are not widely established in the wild in England and are in general restricted to a relatively small number of localized populations, with numbers estimated at between 1500 and 2000 (Harris et al. 1995; Ward 2005; Ward et al. 2008). Small and/or localized populations are found in the Lake District [Bowland], in Northamptonshire and Bedfordshire, with recent colonization of an area around the Oxfordshire/Buckinghamshire/Wiltshire and Gloucestershire borders. Sika deer are found on Lundy Island and on Brownsea Island in the Poole Basin. The largest populations are found in the south, within the New Forest and northern Hampshire, in south-east Dorset, within the Poole Basin; this last population continues to spread westward into Devon and Somerset. Two small populations are reported from the Teifi marshes and from Pendine, near Cardigan in Wales. Figure 29.1 shows the 2016 distribution of sika in Great Britain and Northern Ireland (thus excluding the separate Republic of Ireland) based on surveys carried out by the British Deer Society (BDS).

In addition to these wild, or feral, populations, sika are still widely maintained in deer parks, with an estimated total of about 1000 Japanese sika and a further 500 Manchurian or Formosan sika maintained in private parks (Harris et al. 1995).

Based on the distribution surveys carried out by the British Deer Society in 1972, 2002, 2007, 2011 and most recently 2016 (Fig. 29.1), sika expanded their range within Great Britain as a whole at 5.3% per year between 1972 and 2002 with a 7.3% per year expansion in range between 2002 and 2007 (Ward 2005; Ward et al. 2008). Thereafter the overall rate of spread has settled at around 4% (4.3% from 2007 to 2011; 4.2% from 2011 to 2016; Alastair Ward personal communication). These figures are dominated throughout by the spread of populations in Scotland.

29.3 Population Size

Although there has been no systematic survey of the British Isles sika population, there are local estimates (of varying quality) and some attempts at bringing these together to give an overall approximation (e.g. Harris et al. 1995; Staines 1998). In

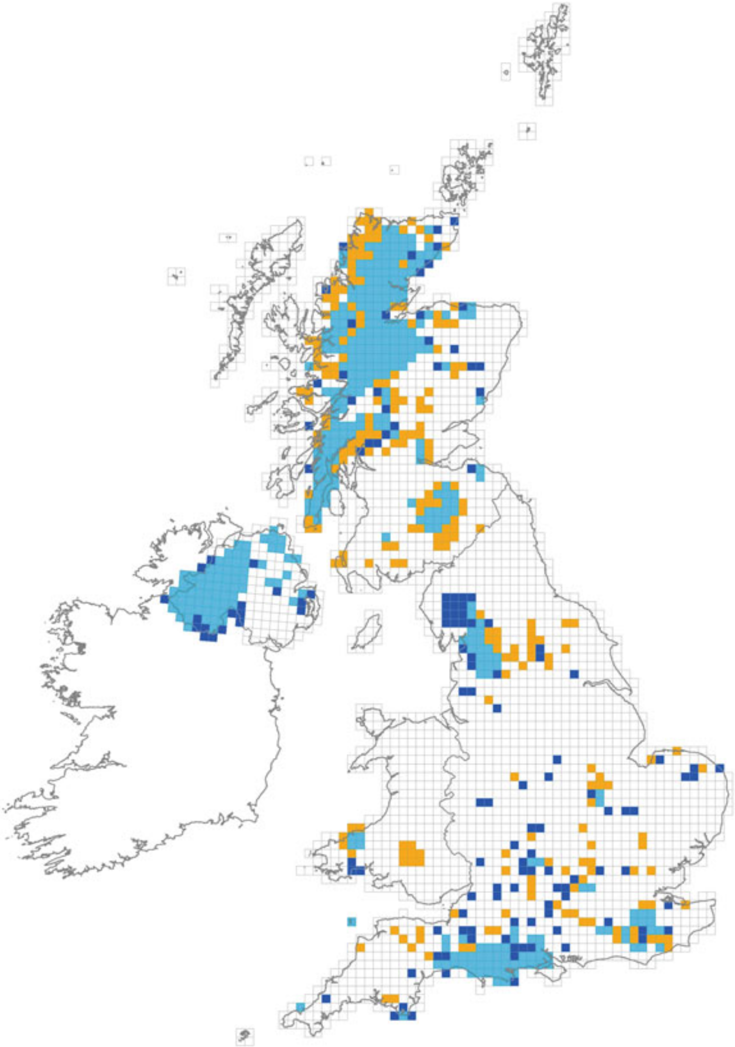

Fig. 29.1 Distribution of sika in Great Britain and Northern Ireland based on surveys carried out by the British Deer Society in 2016 of occurrence of sika in different 10 km grid squares. Dark blue squares show new records for 2016, while light blue squares reflect occurrence reported in earlier surveys and reconfirmed in 2016. Orange squares show where sika were reported in surveys of 2007 and 2011 but were not reconfirmed in 2016. Note however that absence of sightings does not necessarily infer deer were not present. (Map reproduced by kind permission of the British Deer Society)

Scotland, sika have become extremely well established and widespread, with some 14,000 km^2 colonized by the species and an estimated count of around 25,000 individuals (Deer Working Group 2019). At current estimates, the New Forest population numbers about 150–200 animals. Numbers in Bowland are also estimated at around 200 animals (Harris et al. 1995), and fewer than 100 animals are maintained on Lundy Island. The most extensive population in England is that originating in Dorset; this population, which is now extending its range into parts of Devon, probably numbers less than 2000 (Harris et al. 1995; Staines 1998).

Local estimates of the minimum population size are available in many areas of Scotland through Deer Management Group and Forestry Commission records. Densities vary dramatically between forests and counting method, but it is clear that densities are also strongly influenced by forest structure and growth stage (Chadwick et al. 1996). In young plantations, sika deer density was typically between 2.0 and 4.0 deer/km^2, in pre-thicket 4.0–14.0, in thicket 10.3–29.8 and in pole stage and mature forest 8.0–11.0. Densities of sika in other parts of Britain are less well documented. In a managed population at Lulworth in Dorset, densities have been recorded in the region of 11–12 deer/km^2 (Putman and Clifton-Bligh 1997). As elsewhere, substantial populations may build up in suitable habitat. In second rotation forests in County Wicklow, densities of sika ranged from 14 to 44 deer/km^2; in younger forests, estimated densities were equivalent to those recorded in high-density Scottish populations, at 42–45 deer/km^2 (Lowe 1994, unpublished report).

29.4 Social Organization

Outside the breeding season, adult males and females are strongly segregated; in most populations stags and hinds occupy distinct geographical ranges for much of the year. Although commonly considered a 'herding' species, sika are actually one of the less social of the deer species (Putman and Mann 1990).

From the end of winter through until September, the majority of animals are generally encountered alone, or in the case of hinds, a single animal is accompanied by a calf and perhaps a yearling. Thus, in studies in southern England, 95% of females seen through spring and summer were encountered as solitary hinds or single females and followers, and most males were also encountered individually (Mann 1983; Putman and Mann 1990). The rut in September causes an increase in aggregation and increases the number of groups encountered containing adults of both sex; these larger aggregations persist through until March or April, when females drift away from the groups to calve. Even during this winter period however, sika are rarely observed in groups of more than five or six.

Groups appear very temporary associations formed as animals coincide in favoured feeding areas. Observations on marked sika hinds in Wareham Forest in Dorset showed little consistency of group composition or individual association from one day to the next (Horwood and Masters 1970, 1981); these social 'groups' are thus extremely fluid in composition. Group size appears very responsive to habitat; mean group size in denser habitats, such as coniferous woodland or closed oak woods, tends to consist of one or two individuals, with larger groupings generally being encountered in more open habitats (Table 29.1; Putman and Mann

Table 29.1 Typical group sizes recorded in a range of different habitat types in England (from Mann 1983; Putman and Mann 1990)

Habitat	Winter	Spring	Summer	Autumn
Deciduous woodlands	2–3	2	1–2	2–3
Plantation conifer	1–2	2–3	1–2	1–2
Prethicket conifer	2	2	1–2	1–2
Polestage conifer	2	1–2	1–2	1–2
Rides and clearings	2	2–3	1–2	1–2
Heathland	2–6	2–4	2	2–3
Agricultural fields	2–7	2–7	2–5	2–7

1990). Group size even varies in relation to density of different growth stages within commercial coniferous plantations (Chadwick et al. 1996).

29.5 Home Range

Individual deer have relatively small home range areas. In the Killarney National Park in Ireland (a semi-agricultural landscape with open mixed woods of 150–250 ha bordering on larger areas of mixed conifer/broadleaved plantations), mature hinds were found to use ranges of only 18–22 ha; adult stags had somewhat larger ranges (between 45 and 55 ha), and young stags ranged more widely still, within ranges of between 60 and 70 ha (Burkitt in Putman 2000). Based on a sample of animals with movements recorded for 7 years or more, Raymond (2008) reports somewhat smaller ranges still with ranges estimated for stags at between 13 and 41 ha and those for adult hinds from 4 to 9 ha. Radio-tracking studies in two areas of coniferous forestry in northern Scotland suggest range areas of similar extent (C. Maclean, unpublished data, in Putman 2000). On the Arne Peninsula of southern England (an area of coastal heathland and salt marsh), Uzal et al. (2013), using kernel estimation methods, report significantly larger ranges with 90% ranges of mature hinds from 35.51 to 159.85 ha (median 87.67 ha; $n = 21$); in a similar area further inland (Hartland Moor), 90% ranges varied between 58.52 and 137.49 ha (median 107.76; $n = 10$) with an overall median for both sites extending to 89.98 ha ($n = 31$).

29.6 Breeding

Across Britain, sika are seasonal breeders with the rut occurring in autumn, towards the end of September or early October (depending on location and latitude). However, the sika rut is often more protracted than that of other species; whistling males may be heard from the end of August through until mid-December (or exceptionally, as late as mid-February).

Early records of rutting behaviour of sika deer in Britain suggested that males mark and defend mating territories in woodland within the female range (Horwood and Masters 1970, 1981). These territories are marked by fraying and bole-scoring of perimeter trees and thrashed ground vegetation such as heather bushes. More recent study makes it clear however that the mating strategy within sika is extremely flexible, with males adopting a number of different strategies depending on circumstance (Putman and Mann 1990; Putman 1993; Thirgood et al. 1998).

In various populations studied, males have been found to defend rutting territories, as described, but in other cases to collect and defend a harem, as do red deer, or simply patrol areas of superior food quality within the female range and cover oestrous females when encountered (Putman and Mann 1990; Putman 1993). The development of a simple breeding ‘lek’ has also been reported in some central European populations (Bartos et al. 1992). It seems probable that, as in other deer species, males adopt differing strategies depending on the male’s age and dominance status, the density and distribution of females and the degree of competition experienced from other breeding males (Langbein and Thirgood 1989; Putman 1993; Thirgood et al. 1998).

Calves are born from early May to late June after a gestation of around 220 days (Putman 2008). As noted, however, sika have a less well-synchronized breeding cycle than many other British deer species, and it is common to find newborn calves in August or September and, infrequently, as late as October. Normally a single calf is born, but infrequent cases of twin births have been reported (Davidson 1990; Clinton et al. 1992).

Most females breed successfully for the first time as yearlings, i.e. they conceive at 16–17 months and calve around their second birthday and thereafter breed each adult year. In three English populations, New Forest, Lulworth (East Dorset) and Bovington, conception rates among yearling females were around 80%. Those among adult females were 80% (New Forest) and 90% (Dorset populations), respectively (R. Putman, unpublished data; Putman and Clifton-Bligh 1997). In six sika populations studied across Scotland, fertility rates were equally high with yearling conception rates 80% or above and pregnancy rates among adults mostly between 85% and 100% (Chadwick et al. 1996). Pregnant calves were recorded occasionally in animals culled throughout most Scottish and many English populations (Chadwick et al. 1996). Whether or not these precocious breeders would have been able to maintain the pregnancy to its full term, or successfully rear the resultant calf, is less certain.

Reproductive rates are clearly extremely high, and there is no clear evidence for any density-dependent reduction in fecundity among British sika (Putman et al. 1996; Chadwick et al. 1996; Putman and Clifton-Bligh 1997) with recorded densities up to 35 deer/km^2. By contrast, from a long-term study of an unculled sika population on the Muckross Peninsula of southern Ireland, Raymond (2008) found a reduction in the number of adult females observed pregnant, and in the number of culled females found pregnant, with increasing population density. In this population, sika numbers increased from 62 (32 deer/km^2) to 106 (54 deer/km^2) between 1992 and 2000, and this was followed by a sharp rise to 181 (92 deer/km^2) in 2003.

Density of mature sika accounted for 52% of observed variation in pregnancy rates in culled animals (Raymond 2008) and also affected the proportion of yearling females becoming pregnant.

Recruitment rates to the adult population, however, are not as high as such high fecundity rates might suggest. Studies in their native habitat in Japan (Ohtaishi, 1978, Ueno et al. 2018) and in Killarney (O'Donoghue 1991; Raymond 2008) suggest there is a high early juvenile mortality, and only 40–50% of calves may survive to the beginning of their first winter. At present it is unclear to what extent the various populations suffer from density-dependent responses in fertility or survivorship. Because most sika populations in Britain are now managed intensively by hunting or culling, the effects, if any, are likely to be less common.

29.7 Population Dynamics and Dispersal

While populations in northern Scotland are expanding relatively rapidly, both in numbers and distribution, populations in England and in some parts of western Scotland are spreading relatively slowly. This difference in rates of spread—with rapid increases in some populations but not others—seems to reflect the availability of suitable habitat for colonization, particularly the availability of young coniferous plantations. To a lesser extent, landscape features such as roads, railways and urban settlements impede dispersal (Livingstone 2001). In continuous areas of good habitat, sika show a steady expansion in range, estimated in Argyll at between 3 and 5 km per year. In other areas, where rather localized populations occupy smaller pockets of suitable habitat, there appears a rather different pattern of dispersal with long periods of no movement at all beyond the established range, followed by a sudden and rapid irruption from this source (Putman 2000).

In either case, it is characteristically young males that disperse first. At the leading edge of a wave of expansion, young males are encountered at a considerable distance away from the main population centre, and adult males may typically become established in a new area about 10–15 years before the first females are noted (Ratcliffe 1987; Staines 1998).

29.8 Habitat Selection

British sika deer seem primarily associated in their distribution with acid soils, with the majority of populations established in areas of coniferous plantations and adjacent heath. Some idea of the relative preference shown by sika for different forest structures may be seen in an analysis of the range of densities which have been recorded in coniferous forest areas of different growth stages (Chadwick et al. 1996). Sika are adaptable, however, and may be encountered in a wide range of other habitats, including estuarine reed beds and similar wetland areas (e.g. at Arne in

Dorset). Nevertheless, sika deer appear to be dependent on some presence of woodland cover and seem less able to adapt to completely treeless conditions than red deer in upland Scotland (Staines 1998).

In their most ‘typical’ British habitat of acid coniferous woodland, sika show a very predictable pattern of habitat use, lying up in dense thickets during the day and moving out to feed during the night in more open communities within the forest itself or on open ground beyond. This regular pattern is maintained throughout the year; indeed the overall pattern of use of available habitats changes little between seasons (Mann and Putman 1989a). Within the New Forest and associated range in southern Hampshire, sika deer occupy a more varied environment of acid grasslands, heathland and extensive areas of broadleaved as well as coniferous woodland. While the general pattern of habitat use remains much the same as in other areas, the animals make greater use of deciduous woodlands for feeding and make far less use of open fields and heaths (Mann and Putman 1989a).

29.9 Diet

Most studies of sika deer diets have been carried out in coniferous forest and heathland habitat. All show a high intake of grasses and heather (*Calluna vulgaris* and *Erica tetralix*) in all seasons, although the proportion of grasses to heather differed between studies: 30:50 (Mann 1983; Mann and Putman 1989b) 60:20 (Quirke 1991) and 70:20 (Mann 1983). A variety of other dietary components contributed to the remainder of the diet (pine needles, bark and gorse *Ulex europaeus*), but with no single item comprising more than about 8% at any time (Mann and Putman 1989b).

Few comparable data are available for reed bed populations or others, but see Diaz et al. (2004). New Forest sika, however, showed striking differences in diet (Mann and Putman 1989b). New Forest animals consumed considerable quantities of both deciduous and coniferous browse, particularly in the winter, when it comprised up to 23% of the total food intake. In addition, the animals showed striking seasonality in diet, feeding opportunistically on a number of foods as they become available. In spring and summer, New Forest sika fed extensively on grasses and heather—as do populations elsewhere in Britain—but their diet was far more varied. It included significant amounts of forbs, deciduous browse, gorse and conifer needles. In autumn, only 25% of the diet was composed of heather (primarily *Calluna vulgaris*, but including *Erica tetralix* and *E. cinerea*) and grass, with the bulk of the food intake being composed of coniferous browse, gorse, holly and acorns. In winter, there was a further increase in the intake of pine needles when less than 20% of the diet was made up of grasses (Mann and Putman 1989b). These results suggest that sika deer shift diets to obtain the most nutritious food available at any given time in a given place.

29.10 Impacts of Sika on Their Habitat

Because sika deer eat both deciduous and coniferous trees, and heather, they are capable of having browsing impacts on forestry similar to red deer. However, sika deer appear to preferentially be a grazing species, and they have a smaller body size than red deer. Consequently, they may cause less browse damage per capita than do red deer, although there is little question that significant damage may occur in areas of high population density (e.g. Lowe 1994, unpublished report).

Where suitable woodland cover is available, sika tend not to be observed so commonly in open habitats, so at present they are not responsible for trampling damage to upland moorland or blanket bog communities as red deer may be (Scottish Natural Heritage 1994). However, significant impacts have been recorded in salt marsh and open fen communities in southern England (e.g. Diaz et al. 2004). Sika deer do graze on agricultural fields that border woodlands in which they are resident. Local populations have been recorded as causing damage to arable crops in England, although here, because populations are only locally distributed, damage to crops is likewise only likely to be of very local significance (e.g. Putman and Moore 1998; Packer et al. 1999).

29.10.1 Damage to Timber Crops

Like red deer, sika may cause considerable damage to commercial forestry (Ratcliffe 1989; Chadwick et al. 1996; Abernethy 1998; Lowe 1994, unpublished report). Damage may be caused through browsing of both lateral and leading shoots, much as by red deer in similar contexts, and also by bark-stripping in hard winters. The economic significance of such damage may be locally very considerable.

One formal assessment of the extent of damage which may be caused by sika in commercial forestry has been carried out in five coniferous forests in Wicklow, Ireland (Lowe 1994, unpublished report). These forests were planted primarily with Sitka spruce, Douglas fir, Scots pine and larch. Between 22% and 76% of newly planted trees were found to have had their leading shoots damaged by sika. Damage proved most serious in newly established forest in its first rotation. Within the second rotation forests of more varied age structure, leader browsing was recorded on 22–47% of trees, with damage of actual economic significance caused in up to 29% of cases. Older trees also suffered significant bark-stripping damage on the main stem and lower branches, with between 14% and 27% of trees affected in the so-called ‘thicket’ stage of growth before thinning and up to 32% of mature trees still showing significant damage just prior to felling (Lowe 1994, unpublished report).

An assessment of bark-stripping damage by sika in Craggan and Loch Coire forests, Sutherland, showed that the percentage of damaged trees varied between 10.0 ± 9.3% and 75.5 ± 6.9%, dependent on forest block. Lodgepole pine (mean

51.8% damaged) appeared more vulnerable than Sitka spruce (10% damaged) or Scots pine (0.0% damaged) (Forestry Commission for Scotland, unpublished data).

Mature trees may also suffer additional damage in some areas through ‘bole-scoring’ when sika stags gouge deep vertical grooves into the bole of particular trees during defence, marking and advertisement of mating territories in the rut. Such bole-scoring damage appears to be a peculiarity of sika (Larner 1977; Carter 1984).

Despite the equal potential for damage to native woodlands, there are comparatively few reports to date of sika causing significant damage to woodlands in conservation areas in the United Kingdom (e.g. Putman 1995) although damage is considered significant within oak woods and yew woods in Killarney, Republic of Ireland (Larner 1977). Despite the greater abundance of sika in Scotland than elsewhere within the United Kingdom (above), there are likewise no reports to date of damage on open habitats of upland systems (moorlands, upland bogs, arctic-alpine or montane assemblages). However, sika populations at high density are considered to be causing significant damage to internationally recognized salt marsh and fenland communities in Poole Harbour in southern England (Diaz et al. 2004) where heavy grazing caused pronounced structural changes in the vegetation and led to exposure of bare ground.

29.11 Competition with Other Deer Species

There is obvious potential for competition between all deer species in Britain as they overlap in geographical location and in use of food plants. Sika deer are sympatric with red deer in most areas with the exception of the Borders in Scotland and in parts of England. They are generally sympatric with roe deer in England and Scotland and with fallow deer in most of their English range, in North Argyll and Perthshire. In all these cases, there is potential for feeding competition, and with red-sika populations, there is also the possibility of mate competition.

Only one study has so far been published that more objectively explores patterns of habitat use and diet of sika in sympatry with other deer species. In the New Forest, in southern England, Putman (1986, 1996) considered overlaps in habitat use and diet of New Forest sika deer with sympatric populations of fallow, red and roe deer (and free-ranging populations of horses and cattle). Overlaps in habitat use were highest with fallow deer and roe, most notably in autumn and winter (niche overlap 0.80–0.90, falling to 0.65–0.75 in spring and summer). Overlaps in diet were highest with fallow and red deer (fallow, consistently 0.80–0.90; red 0.90–0.95), while overlaps with roe deer were lower (between 0.52 and 0.63 in different seasons). Despite this overlap in habitat use and diet, no direct evidence was found to suggest direct competitive effects in terms of population dynamics (Putman and Sharma 1987), perhaps because population numbers of all species are strongly controlled by (human) management and, thus, kept below levels at which resources become limiting and competition would be apparent.

In long-term studies of the ecology of populations of both sika and red deer in different management blocks in Killarney, Ireland, Burkitt (2009) reported that when sika density was high, calculated overlap in habitat use with sympatric red deer was lower than in sites where sika density was low, suggesting some degree of niche shift at high densities. Both species continued to use their preferred habitats but in significantly different proportion. Proportionally, sika made most use of successional habitats (regenerating woodland or coniferous plantations <15 years) and open high forest, while red deer used more open habitats and actively clearly avoided successional habitats, suggesting that increased numbers of sika were leading to competitive interactions between red and sika causing habitat shifts for both species but most markedly in red deer. The effects of sympatry, even in sites where the density of one or other species was higher than the other, did not alter diet selection of either red or sika deer.

While shifts in habitat use in relation to increasing density of both species were more marked in red deer, there would nonetheless appear to have been an actual competitive effect in terms of suppressed productivity. Raymond (2008) reports for the same populations that body condition of adult male sika, yearling males and yearling females (as reflected in kidney fat index: KFI) was affected more significantly by density of red deer in the same area than by density of sika. Both pregnancy rate and annual post-winter recruitment of juveniles also showed significant negative correlation with density of red deer in a given block (Raymond 2008).

29.12 Hybridization with Red Deer

It has been known that Japanese sika and European red deer can hybridize since an 1884 report by Viscount Powerscourt to the Zoological Society of London (Powerscourt 1884). Although F1 and other early-generation hybrids are readily identifiable from appearance, repeated backcrossing makes it hard to identify most later-generation hybrids. Genetic markers can be used to diagnose hybridism, but even here it can be difficult, since the number of diagnostic markers required to detect introgression doubles with each generation of backcrossing. As genetic tools have improved, surveys have employed increasing numbers of markers, and the picture has gradually become clearer.

In Ireland, the population around Wicklow has been repeatedly demonstrated to be a hybrid swarm, using rocket immunoelectrophoresis (Harrington 1979), nine variable microsatellite loci plus mitochondrial DNA (mtDNA) (McDevitt et al. 2009) or 22 diagnostic microsatellite loci plus mtDNA (Smith et al. 2014). Both microsatellite studies found individuals that were apparently pure sika at the nuclear microsatellite markers, but carried red deer mtDNA, indicating extensive backcrossing beyond the reach of the microsatellite markers, which is consistent with immunoelectrophoresis results suggesting that all Wicklow deer are admixed. It is not clear whether the Wicklow swarm is the result of hybrids escaping

Powerscourt Park or hybridization after escape of sika into red deer range. In contrast, the same set of studies indicate that the sika and red deer in Killarney are not hybridized, although hybrids are present in adjacent Cork, possibly due to a more recent introduction (Smith et al. 2014). Other Irish populations have been less well sampled, but there is evidence of hybrids in Mayo and Galway (McDevitt et al. 2009).

In Scotland, a succession of genetic studies has demonstrated a large hybrid swarm in Kintyre, Argyll (Abernethy 1994; Goodman et al. 1999; Senn and Pemberton 2009; Smith et al. 2018; McFarlane et al. 2020). In the most recent study, a panel of 45,000 single nucleotide polymorphism (SNP) loci from throughout the nuclear genome found that 222 of 513 sampled Kintyre deer (43%) were hybrid, many of them very intermediate (McFarlane et al. 2020), reclassifying 26% of the pure species deer compared to a panel of 22 diagnostic microsatellites (Smith et al. 2018). This reflects the greater amount of backcrossing that is detectable with so many more markers, but it is salutary that there were still an additional nine individuals which tested pure sika on 45K nuclear SNPs but carried red deer mtDNA (McFarlane et al. 2020). Over an 18-year time frame and using microsatellites, the Kintyre hybrid swarm appeared to be static (Senn et al. 2010a). The body size of Kintyre deer correlates with their degree of admixture (Senn et al. 2010b), but stalkers nevertheless find it very hard to discriminate hybrids from pure species individuals (Senn and Pemberton 2009). Elsewhere in Scotland, the 22-microsatellite study found evidence of modest amounts of introgression from long past hybridization in the north-west highlands (Smith et al. 2018), confirmed by the 45K SNP marker panel, which found 4 out of 108 sampled deer were hybrids (3 very sika-like and one red-like); there were also 4 individuals with sika nuclear genomes but red mtDNA (McFarlane et al. 2020). No hybrids were found in the central highlands of Scotland or the Hebrides using microsatellites (Smith et al. 2018). The main area of Scotland that has not been surveyed genetically with modern tools is Dumfries and Galloway, where a few phenotypic hybrids have been reported, presumably the result of the Peebles sika population reaching the Galloway red deer.

In England, early studies of cranial morphology (Lowe and Gardiner 1975; Ratcliffe et al. 1992; Putman and Hunt 1994) suggested that most populations of sika deer were of hybrid status, with the possible exception of the population in the New Forest of Hampshire. Diaz et al. (2006) subsequently investigated the genetic status of a number of sika populations in southern England with six variable microsatellite markers. Based on analysis of 329 samples collected from all over Purbeck, they found extensive evidence that the Dorset population is of hybrid status; populations from the New Forest in Hampshire showed far less evidence of introgression, with any red deer markers of ancient, rather than more recent, origin and at levels no greater than might be accounted for by natural variation/mutation. It would be useful to reanalyse these English sika populations with a larger panel of markers.

Although no overall significant genetic differences were found between the New Forest and Purbeck populations of sika, New Forest deer were more tightly clustered around the range of genetic variation exhibited by control samples obtained from Japan. It is further clear that relatively small numbers of individuals of the New Forest sika contained detected introgressed red DNA. While it is not possible to attach confidence interval to these findings, these small, but perhaps important, genetic differences between the populations support earlier deduction based on cranial morphometrics (Putman and Hunt 1994) that New Forest deer may be more pure sika than other populations of feral sika in the British Isles.

A sample of phenotypic red deer from the English Lake District was included in the recent genetic survey of Scottish populations that used 22 diagnostic microsatellites. Just 3 of 134 individuals appeared to harbour sika genes, all at very low frequency (Smith et al. 2018).

29.13 Management Implications

Given the overall phenotypic similarities of hybrid and non-hybrid deer, whether red or sika, in most British Isles populations, it is not surprising that managers have found differentiating between the two almost impossible (Senn and Pemberton 2009; Smith et al. 2014).

As most hybrids and non-hybrids cannot be identified visually, the selective culling of hybrid deer is not a practical option, unless it is targeted at a local population containing early-generation, obvious hybrids. Once a population has progressed to multiple generations of backcrossing, a selective approach will not be effective. An alternative would be to eliminate a population known to contain hybrids in its entirety. As the spread of sika, and subsequent hybridization, is associated with the distribution of forests, it appears that the only practical way to slow down the spread of sika and their genes is to restrict afforestation in some areas, as previously suggested by Ratcliffe (1987).

Because of their potential for hybridization with red deer and the damage that may be caused to forestry interests once populations reach significant population density, there has long been concern about control of sika populations within Britain (Abernethy 1998). Many populations are already closely managed in an attempt to maintain low population sizes, prevent further increases or actively reduce populations. In Scotland, the major governmental organizations concerned with deer regard sika as a considerable threat, particularly to forestry and due to hybridization, and are actively promoting a policy of rigorous control (Abernethy 1998). Sika deer have been added to Schedule 9 of the Wildlife and Countryside Act [1981, as amended 1998], such that translocation of sika to areas outside their existing range is now illegal in any part of Britain, as is translocation of any deer of the genus *Cervus* to various Hebridean islands.

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Chapter 30
History and Management of Sika Deer on the Delmarva Peninsula

Jacob L. Bowman, T. Brian Eyler, David M. Kalb, and Angela Holland

Abstract Clement Henry accepted a gift of five sika deer from the Duke of Bedford in 1916. After being released on James Island, Maryland, this population became the founders of the current population of 10,000–20,000 individuals on the Delmarva Peninsula. These deer are from the smallest subspecies of sika deer (*Cervus nippon yakushimae*), which are native to Yakushima Island and Kuchinoerabujima Island in Japan. These deer are small in stature with adult body mass of 25–40 kg. Although they are a valuable game species with 3,500–4,000 individuals harvested annually, they are non-native and may compete with the native white-tailed deer. Empirical evidence exists for interspecific competition via overlap in resource use and changes in resources use; however, no evidence exists for interspecific competition impacting population ecology of white-tailed deer. The current management philosophy of the state wildlife agencies is to slow or prevent the range expansion of sika deer to minimize impacts to native white-tailed deer and to reduce human conflicts.

30.1 Introduction and History on the Delmarva Peninsula

Sika deer have three free-ranging populations in the United States. The central Texas population occupies 11 counties with approximately 4,000–5,000 individuals (Feldhamer and Demarais 2009). The Kentucky population of <100 animals is spread across 3 northern counties (Feldhamer and Demarais 2009). The largest population is found on the Delmarva Peninsula, which encompasses Delaware and

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J. L. Bowman (✉) · A. Holland
Department of Entomology and Wildlife Ecology, University of Delaware, Newark, DE, USA
e-mail: jlbowman@udel.edu; aholland@udel.edu

T. B. Eyler
Wildlife & Heritage Service, Department of Natural Resources, Clear Springs, MD, USA
e-mail: brian.eyler@maryland.gov

D. M. Kalb
Rhode Island Fish and Wildlife, West Kingston, RI, USA
e-mail: David.Kalb@dem.ri.gov

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the Eastern Shores of Maryland and Virginia. This population numbers approximately 10,000–12,000 individuals. The majority of this Delmarva population is found in Maryland, which accounts for 85–95% of the population.

The origin of sika deer on the Delmarva Peninsula was traced to Yakushima Island, Japan, using genetic evidence (Kalb and Bowman 2017; Kalb et al. 2019). These deer are from the smallest subspecies of sika deer (*Cervus nippon yakushimae*), which are native to Yakushima Island and Kuchinoerabujima Island in Japan (Kalb and Bowman 2017). Kalb and Bowman (2017) detailed the probable route of the descendants of the deer moving from Japan through Europe into Woburn Abbey in England. In 1916, the Duke of Bedford gave five individuals to Clement Henry in Dorchester County, Maryland (Kalb and Bowman 2017). These deer were kept as pets for a short period before being released onto James Island (Fig. 30.1; Kalb and Bowman 2017).

The population on James Island continued to increase in abundance and numbered 280–300 individuals by 1955 (Christian et al. 1960; Flyger 1960). Local residents reported that sika deer were common on Taylors Island, to the south of James Island, and were established on the mainland (Flyger and Warren 1958). In August 1957, an uncontrolled wildfire burned across much of James Island reducing deer forage (Flyger and Warren 1958). The following winter, 1957–1958, was particularly severe, and a mass die-off of sika deer occurred on the island. Flyger and Warren (1958) found 161 skeletal remains of deer sika, which accounted for 50% loss of the population on James Island. The population on James Island continued to decline over time as the size of the island decreased and eroded into three smaller islands (Kalb and Bowman 2017).

By 1962, sika deer occupied the western third of Dorchester County (Fig.30.1; Flyger and Davis 1964). The population has continued to increase in abundance and expand its range. Density of sika deer in western Dorchester County averaged 33 deer/km^2 and ranged from 17 to 42 deer/km^2 (Dougherty 2010; Dougherty and Bowman 2012). By 2021, the Dorchester population had expanded into adjacent counties with breeding populations occurring in Caroline, Somerset, and Wicomico counties in Maryland (Fig. 30.1). The populations in Caroline and Somerset counties are small with <10 sika deer harvested per year. The Wicomico population is larger with >100 harvests per year. The Dorchester population has also expanded into Delaware along the Nanticoke River with a small breeding population in Sussex County, Delaware. This population accounts for one to three harvests per year. Sika stags have been harvested in Kent and Cecil Counties, Maryland, and in Kent County, Delaware. All these stags were yearlings and likely were dispersing individuals.

A second population on the Delmarva Peninsula is on Assateague Island, which is a barrier island that stretches along the southern coast of Maryland and the northern coast of Virginia (Fig. 30.1). In 1920, Charles Law purchased five sika deer from the James Island population (Flyger 1960; Kalb and Bowman 2017). These deer were kept in Berlin, Maryland, as pets for few years before they and their offspring were sold to Dan Trimper in Ocean City in 1924 (Kalb and Bowman 2017). These deer were part of a roadside amusement park, but at some point, they were released onto

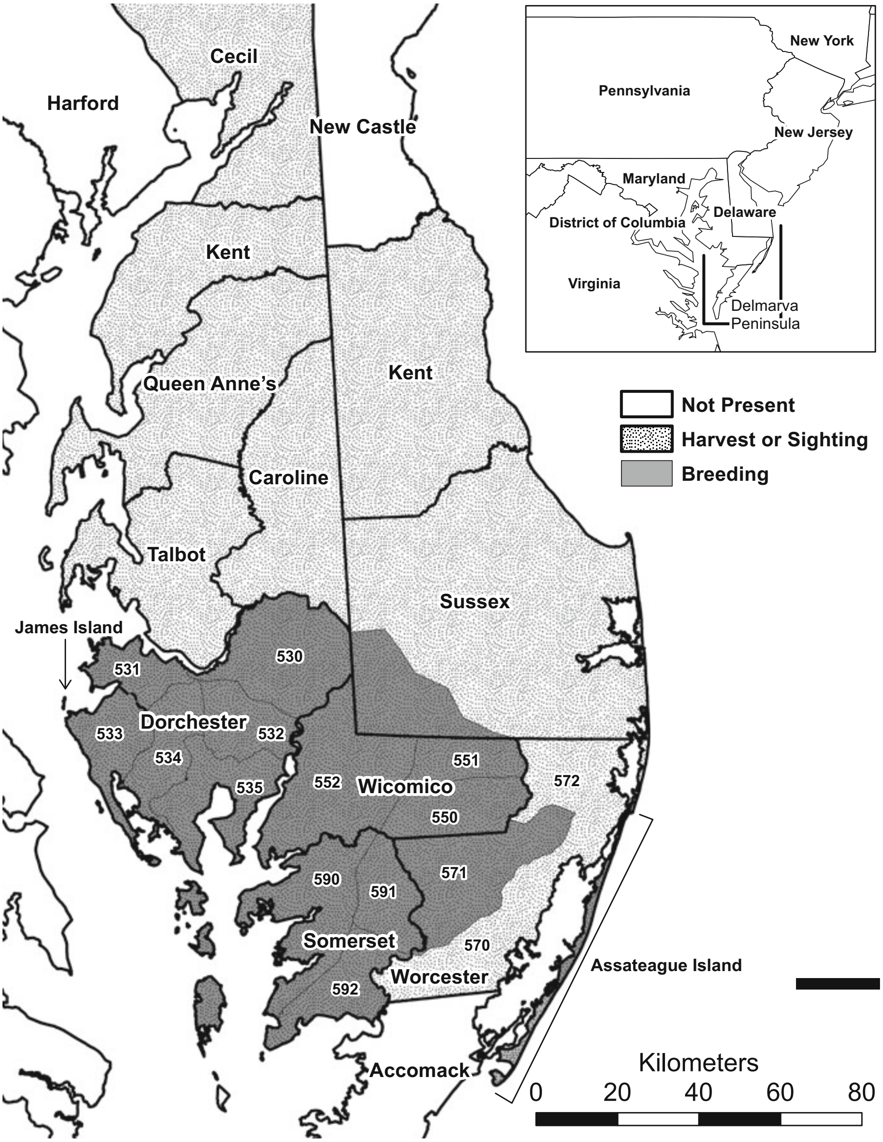

Fig. 30.1 The breeding range of sika on the Delmarva Peninsula in 2021. The numbered subsections in the counties are the private land codes used to track deer harvest

the northern end of Assateague Island (Kalb and Bowman 2017). This population expanded south into the Virginia portion of the island by 1943 (USFWS 2015). In 1958, estimates of the population ranged from 60 to over 100 individuals, but these estimates were likely gross underestimates (Presnall 1958; Flyger 1960). The population had reportedly grown to 1,000 individuals by 1962 (Flyger and Davis 1964).

By 1963, the sika deer population was estimated to be 1,300 individuals, which caused a clear browse line on the island (USFWS 2015). The Chincoteague National Wildlife Refuge (the Virginia portion of Assateague Island) initiated a harvest to reduce deer numbers in 1964 (USFWS 2015). The deer population on the Chincoteague NWR was estimated at 1,000 individuals in the mid-1990s. The current population estimate for the entirety of Assateague Island is 1,000–2,000 sika deer. A small population of sika deer is believed to inhabit the Maryland mainland adjacent to the island (Worcester County, Deer Management Units 570 and 572, Fig. 30.1), but it is unknown if there is a breeding population. Sika deer are not believed to occupy the mainland in Virginia.

30.2 Biology and Ecology

30.2.1 Genetics

The Delmarva population of sika deer originated from the island of Yakushima Island stocks and came by way of the United Kingdom (Kalb and Bowman 2017; Kalb et al. 2019). The introduction was a single release of five individuals (Kalb and Bowman 2017; Kalb et al. 2019). This population has reduced genetic variation resulting from founder and bottleneck events (Kalb et al. 2019). Although the population has lost neutral density from these events, the population does not exhibit any known physical abnormalities associated with inbreeding (Kalb et al. 2019).

30.2.2 Description

Sika deer exhibit a range of color patterns. They are typically chestnut brown in winter and more reddish brown in the summer with a dark stripe along the spine (Whitaker Jr and Hamilton Jr 1979). They often have seven to eight rows of white spots, which are more obvious in the summer and along the spine (Whitaker Jr and Hamilton Jr 1979). They exhibit a large white rump patch throughout the year (Whitaker Jr and Hamilton Jr 1979).

The sika subspecies introduced into Maryland is a small island subspecies and much smaller than their mainland counterparts. Stags obtain the maximum body size at 5.5–7.5 years (Feldhamer et al. 1985). Adult body mass is 30–40 kg with very large individuals exceeding 45 kg (Feldhamer et al. 1985). Total body length is 135–145 cm with a shoulder height of 78–84 cm (Feldhamer et al. 1985). Antler development follows patterns like other cervids. Antlers begin growing in May and harden in August. Antlers are retained until spring when they are shed. Young stags (0.5 years old) have button, and yearlings (1.5 years old) almost always have spike antlers. Adult stags have two to three points per antler beam with exceptional individuals having four points per antler beam (Whitaker Jr and Hamilton Jr 1979;

Feldhamer and Demarais 2009). Antler beam on mature males are 30–60 cm in length and 2.5 cm in diameter (Whitaker Jr and Hamilton Jr 1979). Hinds reach maximum body size earlier at 4.5–5.5 years (Feldhamer et al. 1985). Adult body mass is 25–35 kg (Feldhamer et al. 1985). Total body length is 122–128 cm with a shoulder height of 66–68 cm (Feldhamer et al. 1985). Most adult mortality is harvest related (Eyler 2001; Kalb 2010). Stags typically survive 1.5–3.5 years, with some living longer than 7 years (TB. Eyler, unpublished data). Hinds typically survive 1.5–5.5 years with some documented surviving 20+ years (TB. Eyler, unpublished data).

30.2.3 Reproductive Ecology

Rutting activity begins in late September and can continue into December with a peak in the middle of October (Feldhamer 1980; Mullan et al. 1988). Although hinds can breed at 6 months of age, most do not breed for the first time until they are 1.5 years old (Mullan et al. 1988). Adult hinds ovulate before yearlings, which likely extends the calving season (Feldhamer and Marcus 1994; Mullan et al. 1988). The conception rate is very high for adults and yearlings (94.4%, Mullan et al. 1988). The gestation period is 30 weeks with most parturition occurring in late May and June (Feldhamer 1980). Typically, single calves are produced with twins being extremely rare (Feldhamer 1980; Feldhamer and Marcus 1994). The size and weight of neonates on the Delmarva Peninsula are unknown.

30.2.4 Diet

The diet of the sika deer is flexible, likely resulting from their rumen physiology (Feldhamer and Demarais 2009). Sika deer diet during winter on the Delmarva Peninsula is forbs (1–3%), grasses (42–47%), sedges and rushes (12–16%), and woody browse (38–40%; Kalb 2015, Kalb et al. 2018). The most unique characteristic of their diet on the Delmarva Peninsula is the abundance of saltwater and freshwater marsh species (e.g., *Carex* spp., *Cyperus* spp., *Juncus* spp., *Scirpus* spp., *Phragmites australis*, *Spartina patens*; Kalb 2015; Kalb et al. 2018). This diet corresponds to them being more common in tidal marsh and bottomland areas. They also are responsible for crop depredation on corn and soybeans, which can be important food sources during the growing season.

30.2.5 Diseases and Parasites

Sika deer are host to a wide variety of diseases and parasites (Feldhamer 1980). Davidson and Crow (1983) reported that sika deer in Maryland and Virginia were less burdened with ticks, chiggers, and sarcocystis than native white-tailed deer, but sika deer in their original distribution area (i.e., Japan) were burdened by ixodid ticks (Yamauchi et al. 2009). Likewise, serology examinations of the same animals suggested that sika deer were exposed to fewer infectious disease agents than native whitetails. Feldhamer and Demarais (2009) summarized the little that is known about diseases and parasites within the introduced population in North America, much of which is from outside of the Delmarva Peninsula. A respiratory virus, *Myxovirus parainfluenza* 3, was detected via antibodies of sika deer from Assateague Island, but population level effects are unknown (Shah et al. 1965). Lyme disease is common on the Delmarva Peninsula. Deer are known reservoirs of *Borrelia burgdorferi* the causative agent of Lyme disease, and antibodies for it were detected in sika deer from Assateague Island (Oliver et al. 1999). Although deer serve as reservoirs of the pathogen, they do not exhibit any impact on their survival. Hemorrhagic disease is an important cause of mortality in white-tailed deer and typically occurs in outbreaks every 6–8 years (Haus et al. 2020). White-tailed deer on the Delmarva Peninsula exhibit annual survival rates of 72–98%, but annual survival rates as low as 38% have been observed in outbreak years (Haus et al. 2020). Observations by biologists in Maryland suggest that sika deer may not be impacted by hemorrhagic disease since the virus has not been identified in the species to date. Chronic wasting disease has been detected in Maryland white-tailed deer in the western part of the state, and the disease has been detected in captive sika deer elsewhere. While this disease has not been detected in Maryland or Virginia sika deer, biologists assume sika deer in these states are susceptible to the disease.

30.2.6 Vocalizations

Sika deer are often noted as being the most vocal cervid with upwards of ten vocalizations identified (Feldhamer 1980). The most common is an alarm call used by both sexes which is akin to a “sharp scream” (Feldhamer 1980). During the rut, stags vocalize a roar, which is common in other species of *Cervus* and has been described as “blood-curdling screams” in sika deer (Feldhamer 1980). The hinds are reported to communicate via “goatlike bleats” and to use “soft horselike neighs” when communicating with calves.

30.2.7 Spatial Ecology and Habitat Use

Sika deer are nocturnal and exhibit very little movement during the day (Feldhamer 1980). They are solitary except for hinds with calves (Whitaker Jr and Hamilton Jr 1979). Stags sometimes form bachelor groups after antler shedding (Whitaker Jr and Hamilton Jr 1979). Hind home ranges averaged 161 ha in Dorchester County, Maryland (range 35–546; Eyler 2001). Only 1 of 15 hinds dispersed suggesting a low dispersal rate for hinds (Eyler 2001). For stags, home ranges were highly variable in size and ranged from 464 to 4121 ha and were influenced by season and deer movement (Kalb 2010; Kalb et al. 2013). Stags exhibit three home range types: local, migratory, and nomadic (Kalb 2010; Kalb et al. 2013). The most common movement group (70%; 42 of 60) was local, and these deer exhibited short movements confined to a well-established home range (Kalb 2010; Kalb et al. 2013). Migratory stags (14 of 60) had well-defined seasonal movements between 2 distinct home ranges (Kalb 2010; Kalb et al. 2013). Nomadic stags (4 of 60) were least common and exhibited movements across the landscape without an association to season (Kalb 2010; Kalb et al. 2013). Most (19 of 20) yearling stags dispersed, but 1 dispersed at 2 years of age (Kalb 2010; Kalb et al. 2013). The average dispersal distance was 7.7 km (Kalb 2010; Kalb et al. 2013). Most stags (55%; 11 of 20) dispersed in the spring with an average date of 23 April (Kalb 2010; Kalb et al. 2013). Some stags (5 of 20) dispersed in summer with an average date of 19 June (Kalb 2010; Kalb et al. 2013). The remaining stags (4 of 20) dispersed in fall with an average date of 30 September.

Sika deer on the Delmarva Peninsula are typically found in freshwater and saltwater marshes and surrounding forests and cropland (Whitaker Jr and Hamilton Jr 1979). Much of what we know about sika deer habitat selection on the Delmarva Peninsula is based on ancillary observations since few studies have been conducted. Female sika deer in Dorchester County, Maryland, selected tidal and fresh marshes and wet woodlands more than other habitats (Eyler 2001). On Assateague Island, sika selected forest and tall shrub more than other habitats (Diefenbach and Christensen 2009). Assateague Island is a unique habitat and is home to white-tailed deer and ponies, which may partially explain differences observed with Dorchester County.

30.3 Interspecific Competition

Interspecific competition between sika deer and the native white-tailed deer has been a concern since the 1970s (Feldhamer et al. 1978). Interspecific competition occurs when the use or defense of limited resources by one species causes the availability of resources for another species to be limited (Feldhamer and Demarais 2009). These relationships are notoriously difficult to document in cervids (Feldhamer and Demarais 2009). Feldhamer and Demarais (2009) noted three ways to document interspecific competition: “(1) overlap in resource use; (2) changes in resources use; or (3) changes in population density, age structure, fecundity, or survival in one or both competing species.”

The earliest empirical evidence for interspecific competition came from Assateague Island, which is a barrier island stretching along the coast of Maryland and Virginia (Fig. 30.1). The diet of sika deer and white-tailed deer had significant overlap with most plant species consumed by both species (Keiper 1985; Keiper 1990). An interesting finding for sika deer diet was the overall lack of grasses in their diets (Keiper 1985; Keiper 1990). Grasses are typically a dominate food item in other areas (Feldhamer and Demarais 2009) but represented less than 25% of their diet on Assateague Island (Keiper 1985; Keiper 1990). The presence of ponies on the island may have confounded these results because ponies are grazers and depend largely on grasses for forage. Keiper (1990) documented that ponies caused a decline in dune vegetation (i.e., grasses), which likely affected grass availability for sika deer. Additionally, the ponies likely reduced the availability of other forage types for both species of deer (Keiper 1990). Sika deer have greater dietary plasticity and are more successful in degraded habitats (Feldhamer and Demarais 2009). The lower white-tailed deer abundance may be a result of habitat degradation by the ponies and not interspecific competition with sika deer.

Understanding how sika deer and white-tailed deer use the landscape in space and time is necessary for understanding interspecific competition. Another study on Assateague Island investigated space-use of both species (Diefenbach and Christensen 2009). Survival rates and harvest rates were similar between the two species (Diefenbach and Christensen 2009). Harvest was the primary cause of mortality, and survival rates outside the hunting season were 98–100% (Diefenbach and Christensen 2009). These results suggest that interspecific competition is not impacting adult survival rates. Home range size of sika deer was greater than white-tailed deer (Diefenbach and Christensen 2009). Sika deer moved longer distances than were observed in white-tailed deer (Diefenbach and Christensen 2009). Diefenbach and Christensen (2009) hypothesized that these longer movements may have permitted sika deer to exploit food resources that were in limited quantity or higher quality, but without an assessment of diet, this hypothesis could not be investigated further (Diefenbach and Christensen 2009). Both species of deer used habitats defined as tall shrub and forest vegetation and were less likely to use areas away from these habitats (Diefenbach and Christensen 2009). These results may have been confounded by the presence of ponies, which use open habitats more than forested habitats. Diefenbach and Christensen (2009) recommended additional research to understand the interspecific competition between both deer species and ponies.

Outside of Assateague Island, research on interspecific competition between sika deer and white-tailed deer has occurred in Dorchester County, Maryland, where these deer are the only species of ungulates (Fig. 30.3). Eyler (2001) used radiotelemetry to investigate spatial use of both species. Female sika and white-tailed deer had similar home range areas (Eyler 2001). Using a 65% core-use estimate, the mean percent overlap within species was 32%, whereas the mean percent overlap between species was 18% (Eyler 2001). Sika deer and white-tailed deer used habitats differently based on compositional analysis of habitat use (Eyler 2001). Female sika deer selected marshes more than other habitat types, whereas female white-tailed deer selected forested habitats (Eyler 2001). Although cropland was the second most important habitat for white-tailed deer, it was the least important for sika deer (Eyler 2001). Based on these results, sika deer and white-tailed deer appear to be partitioning habitat use, which would result in reduced competition (Fig. 30.4).

To better understand dietary overlap, Kalb et al. (2018) collected fecal samples from sika deer and white-tailed deer in three areas with similar habitat quality: (1) an area with sika deer but very few white-tailed deer, (2) an area with white-tailed deer but not sika deer, and (3) an area with similar densities of sika deer and white-tailed deer. These areas were selected to control for harvest pressure and resource availability (Kalb 2015; Kalb et al. 2018). Microhistological analysis was used to estimate the percentage of plant species used by sika deer and white-tailed deer (Kalb 2015; Kalb et al. 2018). The deer species exhibited significant resource overlap (range 63–88%; Kalb 2015; Kalb et al. 2018). When sika deer and white-tailed deer were both present, white-tailed deer niche breadth increased (108%), and diet quality (17%) was lower (Kalb 2015; Kalb et al. 2018). Sika deer and white-tailed deer had a 78% overlap in diet (Kalb 2015; Kalb et al. 2018). White-tailed deer were altering their diet in the presence of sika deer and consuming lower-quality forage. Sika deer are intermediate feeders, which tolerate greater fiber in their diets, whereas white-tailed deer require greater diet quality because they are concentrate selectors (Kalb 2015; Kalb et al. 2018). The changes in niche breadth and diet quality along with significant dietary overlap strongly denote dietary competition between these species.

Hunter harvest across time could provide an understanding of interspecific competition between sika deer and white-tailed deer. In the 1970s, the percentage of sika deer in the harvest increased as white-tailed deer decreased (Feldhamer et al. 1978). Part of this change likely resulted from a reduction in the bag limit for white-tailed deer and an increase in the bag limit for sika deer (Feldhamer et al. 1978). As previously noted, the harvest rates for sika deer and white-tailed deer were similar in 2006–2007 (Diefenbach and Christensen 2009). Data from hunter harvest in Dorchester County dating back to 1990 does not show a significant decrease in white-tailed deer harvest (TB. Eyler, unpublished data). An important limitation of harvest data is that it may not mirror actual changes in the population. The fluctuation in harvest numbers is related to harvest regulations, hunter behavior, and habitat.

In summary, empirical evidence exists for interspecific competition via overlap in resource use and changes in resources use; however, no evidence exists for interspecific competition impacting population ecology of white-tailed deer. Research in Texas suggests the competitive effects may be more pronounced during periods of resource limitations (Feldhamer and Demarais 2009). With the exception of Assateague Island, habitat quality is excellent across the Delmarva Peninsula. This high habitat quality may explain why population level effects of interspecific competition with sika deer have not been observed in white-tailed deer.

30.4 Management of Sika Deer on the Delmarva Peninsula

30.4.1 Maryland

Maryland's annual deer hunting season officially closed in 1902 after the near extirpation of white-tailed deer during the 1800s. The season did not reopen in Dorchester County until 1951. As a result, there was no formal harvest of sika deer for the first 35 years of their free-range existence in Maryland; however, local residents most likely made opportunistic use of the available resource, and there were scattered reports of their harvest as early as 1938 (Flyger and Warren 1958).

Sika deer remained a relatively small fraction of the total deer harvest in Dorchester County during the 1950s and 1960s. From 1951 until 1972, there was no differentiation in sika deer and white-tailed deer in Maryland Department of Natural Resources (MDNR) harvest records (Feldhamer et al. 1978). However, harvest estimates for the period suggest that less than 200 sika deer were harvested annually and comprised less than 20% of the total deer harvest for the county. Although the annual harvest was relatively small during the timeframe, evidence suggested the population was slowly increasing in number and expanding its range. Beginning in 1973, MDNR separated sika deer from white-tailed deer on their hunter harvest tags, enabling better tracking of harvest and population trends for the two species; however, both species still shared the same hunting seasons and bag limits.

The sika deer harvest has steadily increased in Dorchester County since the 1970s, and their harvest exceeded the white-tailed deer harvest for the first time in 2014 when hunters harvested 2,847 sika deer and 2,639 white-tailed deer. Since then, the harvest has increased to over 3,000 sika deer annually (Fig. 30.2). An increasing population, more opportunities to hunt them in the form of longer and more diverse seasons, and their increased popularity as a unique game species are largely responsible for the higher harvests. Maryland is the only state with a sizeable, free-ranging population of sika deer available for hunters. Likewise, the advent of social media has increased awareness of the species, and hunters travel from across the United States to hunt them.

Sika deer hunting seasons (hunting implements and dates) have generally followed those of white-tailed deer in Dorchester County. Early deer seasons prior to 1953 were limited to firearm hunting only. In 1953, the first archery season occurred for white-tailed deer; however, it was not legal to harvest sika deer with archery equipment until 1968. Since that time, both species tend to share the same seasons, but with different bag limits. Along with archery equipment and modern firearms, there is also a designated primitive firearm season (i.e., muzzleloaders), established in 1978, to hunt both species of deer. These additional seasons also provide increased opportunity for hunters to pursue sika during the peak rut.

Over the years, the bag limit for sika deer has varied and ranged from as few as one deer per year when deer hunting resumed in 1951 up to nine deer during the 1980s and today. During the 1980s, the sika deer limit was often more liberal than the white-tailed deer limit in an effort to reduce the population. However, as the

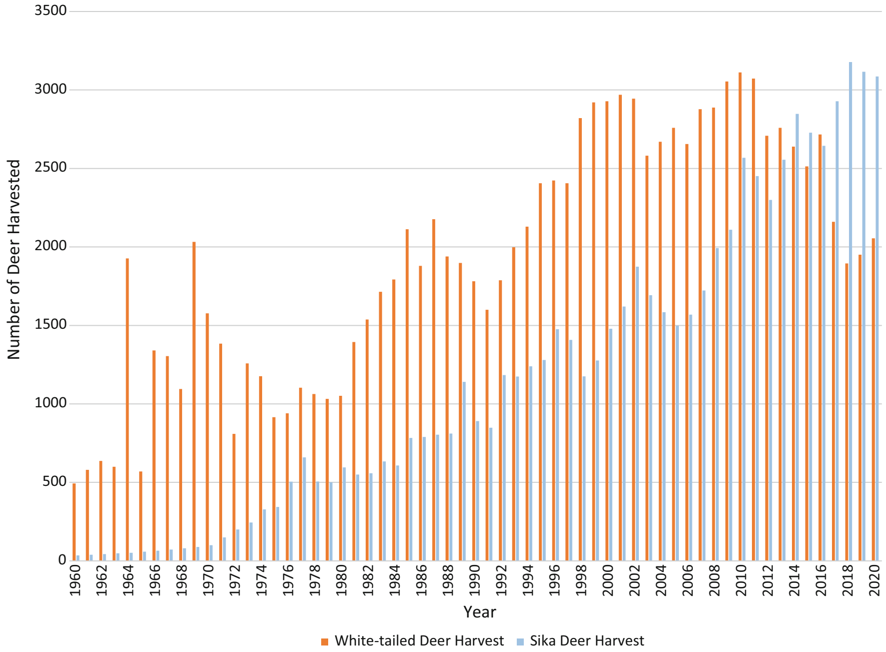

Fig. 30.2 The number of sika deer and white-tailed deer harvested in Dorchester County, Maryland, USA, 1960–2020

Fig. 30.3 Sika deer are more aggressive behaviorally than white-tailed deer. Sika deer acting aggressively towards a raccoon at a bait site for a camera survey

species gained in popularity with hunters and wildlife observers, MDNR revised their approach to sika deer management with a goal of stabilizing the population. Today, sika deer bag limits are more conservative than white-tailed deer limits, but given the harvest patterns of most hunters, who typically only harvest two deer at

Fig. 30.4 Sika deer hinds are smaller than the native white-tailed deer

most, the bag limit is not a controlling factor in the population trend for either species when set above two deer. Instead, the number of hunters in a given year and access to land to hunt sika deer are largely what drives population growth or decline.

MDNR sets seasons and bag limits biennially with the goal of maintaining the white-tailed deer and sika deer population at healthy levels that are compatible with humans and the environment. For sika deer, an underlying goal is to slow the expansion of the species beyond their current range. Flyger and Davis (1964) reported that sika deer had colonized the western third of Dorchester County. Since then, based on MDNR harvest records, the species has colonized nearly all of the remainder of the county and has spread into adjacent counties in some areas. The species is now commonly harvested in the south and east of Dorchester County and in parts of Somerset and Wicomico counties, and a small number are harvested in the northeast of Caroline County and the state of Delaware. Likewise, one individual, a yearling stag, was harvested in Kent County, Maryland, in 2014 and one in Cecil County, Maryland, in 2019, approximately 100 km to the north (Fig. 30.1). However, population expansion most likely has been slowed by a limited amount of preferred habitat, which includes tidal marshes and forested wetlands, and by the geography of the area, which includes several substantial rivers, which likely act as barriers to dispersal. As a result, the population may not be expanding as fast as was once speculated.

A significant number of sika deer remain on Assateague Island off the coast of Maryland and Virginia. Most of Assateague's land area is a federal wildlife refuge in Virginia (Chincoteague National Wildlife Refuge) and a national seashore and state park in Maryland (Assateague Island National Seashore and Assateague Island State Park). All three of these entities offer sika deer hunting as a way to manage the population. In recent years, approximately 200–300 sika deer have been harvested annually from the 63-km^2 island. The annual harvest on the Maryland portion of the island is incorporated into MDNR harvest records.

Sika deer are an important economic resource for Dorchester County. It is estimated that 5,000 hunters pursue sika deer each fall and winter. Many of these hunters patronize the hotels, restaurants, and other stores in the area during a time of year when tourism is otherwise slowing down. Likewise, anecdotal information suggests that real estate and land lease prices are elevated in the county if sika deer are available on the property for hunting. Several guide and outfitter services specialize in sika deer hunting in the county as well. Future and ongoing research by MDNR is focusing on the economic impact of this species.

Like white-tailed deer, sika deer do cause some human conflicts in Dorchester County, predominantly in the form of agricultural damage from browsing crops. Agricultural damage by deer is a prominent issue for MDNR and many other state game agencies. MDNR has a Deer Management Permit (DMP) system that affords agricultural producers the ability to harvest deer on their property year-round if they are suffering damage. In 2019, producers in Dorchester County removed 367 sika deer and 420 white-tailed deer under the DMP system.

30.4.2 Delaware

Sika deer in Delaware do not have a separate season and are harvested during the white-tailed deer season (September 1–January 31). Hunters are required to report sika deer harvests to state wildlife biologists. Only 15 sika deer have been harvested and reported in Delaware as of January 2021. The first harvest was in 2008 with one to three being reported harvested annually, since 2016. Most harvests ($n = 12$) have been in Sussex County (Wildlife Management Zone 13, southwest corner of county), and most have been on or around the Nanticoke Wildlife Area. Harvest reports all sexes and ages in this area suggesting an established breeding population. A few sika deer ($n = 3$) have been harvested in Kent County (Zones 6, west-central part of county, and 8, south-central part of county). All of these harvests were spike antlered stags suggesting they were dispersing individuals and not part of an established population. Delaware's management goal for sika deer is to limit the range expansion in the state.

30.4.3 Virginia

Sika deer on Assateague Island in Virginia are managed via regulated hunting conducted by the Chincoteague National Wildlife Refuge (NWR). The Chincoteague NWR is comprised of approximately 40 km^2 of available deer habitat. Hunting on the island occurs annually in the fall by permit only. The Chincoteague NWR offers both archery and firearms hunting. In recent years, the daily bag limit has been set at five sika deer per hunter (no more than two antlered). Hunters have harvested an average of 195 sika deer per year from the Chincoteague NWR over the past 20 years. The goal of the Chincoteague NWR is to manage sika and native white-tailed deer at population densities that will not degrade the island shrub vegetation by overbrowsing.

30.5 The Future of Sika Deer on the Delmarva Peninsula

Sika deer are an important hunting resource with significant economic benefit for the Delmarva Peninsula. Likewise, they are popular with non-consumptive users who enjoy observing them while enjoying other outdoor activities. However, the state wildlife agencies want to slow or prevent the range expansion of sika deer to minimize impacts to native white-tailed deer and to reduce human conflicts. Crop damage can be a significant issue for agricultural producers on the Delmarva Peninsula, so continued management of the species will be necessary. Hunter harvest will remain the most effective method to maintain sika deer at healthy levels.

Sika deer were introduced on the Delmarva Peninsula over 100 years ago, but we still lack a complete understanding of their ecology in the area. The reproductive ecology including calf survival and timing of calving is necessary to better understand population ecology. Additionally, understanding diseases and parasites that impact sika will also allow us to better understand population ecology. We need additional research addressing their habitat use, so we can better understand what areas they occupy and what areas they might expand into overtime. Finally, we need to continue to research possible interspecific competition with white-tailed deer.

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Chapter 31
The Future of Sika Deer Management in New Zealand: Invasive Deer or Hunting Resource?

Graham Nugent and Campbell Speedy

Abstract As an introduced 'invasive' species, sika in New Zealand are regarded by some as conservation pests and by others as a hunting resource. We trace the history of herd development over the 116 years since sika were first introduced and summarise the changes in the management of the herd. Introduced as a hunting resource, they (and other deer species) quickly became regarded as pests and were subject to population control and then, in a minor way, to commercial hunting. Since the 1980s, however, recreational sika hunting has been predominant. Despite sika being highly valued as a recreational hunting resource, and despite there being no limits on when and how many sika can be harvested, current hunting pressure is insufficient to prevent high sika densities other than in the most readily accessible areas. That results in small body sizes with poor meat yield and/or trophy quality. Those high densities also cause substantial changes in the structure and composition of the native vegetation, so sika (and deer generally) continue to be seen as conservation pests. However, there is too little conservation funding to prioritise action against the unwanted impacts of sika on the local vegetation ahead of more urgent and important threats to indigenous biodiversity elsewhere. The result is poor outcomes both for hunting and for conservation. More active management of at least part of the herd (mainly through increased female harvest) is currently being mooted and could provide better joint outcomes.

31.1 Introduction

Sika (*Cervus nippon*) management (and evolution) in New Zealand has long been controversial. That is because they are not native to New Zealand, so are seen by some as pests but by others (hunters in particular) as a resource. That pest-vs-

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G. Nugent (✉)
Perth, Western Australia, Australia
e-mail: gornugent@gmail.com

C. Speedy
Wildlife Management Associates Ltd, Turangi, New Zealand
e-mail: ngakowhai@xtra.co.nzc

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resource dichotomy of viewpoints is widely recognised (Russell 2014) and has long applied not only to sika but also to the six other deer species introduced to New Zealand (Nugent and Fraser 1993). In this chapter, we document the background to pest-vs-resource controversy and then outline a current initiative to find a workable compromise for future management.

Sika were successfully introduced to New Zealand in 1905 (Banwell 1999). Their introduction came towards the end of the late nineteenth-century wave of introductions by early European colonists who yearned for the mammalian fauna of their home countries (or other places)—New Zealand had no land mammals, so some colonists sought to create hunting opportunities both for sport and for food. Many such introductions successfully established wild populations, with many of the introduced species now regarded as invasive (King and Forsyth 2021).

31.2 Sika in New Zealand: A Brief History

31.2.1 What Are NZ Sika?

The current sika population in New Zealand was established in 1905 by the release of three females (one possibly with a fawn born en route) and one male, imported from Woburn Abbey, England. At that time, at least five different subspecies of sika were being held at Woburn Abbey, and it is believed that at least two, and probably more, of those subspecies were genetically represented in the deer brought to New Zealand (Banwell 2009). Despite apparently stemming possibly from just a single male founder, sika aficionados in New Zealand recognise two male phenotypes (Banwell 2009)—one having black velvet antlers akin to that of one of the Japanese subspecies (*C. n. nippon*) and the other with red/golden velvet characteristic of the Manchurian subspecies (*C. n. mantchuricus*) (Fig. 31.1).

Since release, the population has increased substantially, with some thousands of sika now harvested annually by hunters (CNISF 2015, http://sika foundation.co.nz/, retrieved 14 August 2018). However, sika deer still occupy only about 3.3% of the country, almost all of that in one large area (ca. 9000 km^2) in the centre of the North Island, with only a few small widely scattered populations elsewhere (Fraser et al. 2000). A map of current sika distribution can be accessed via https://deptconservation.maps.arcgis.com/apps/MapSeries/index.html?appid=e61-e0f57d06a4663b7cd19a5bba53059 (accessed 26 June 2021). In comparison, sika are outnumbered by the introduced red deer (*Cervus elaphus*), which now occupy −154,000 km^2 (−58% of New Zealand), and introduced fallow deer (*Dama dama*) (−28,000 km^2) (King and Forsyth 2021). Most or all of the most outlying populations of sika are likely to have been established in the last few decades by hunters wishing to establish new hunting opportunities (Fraser et al. 2000) even though such releases are illegal under New Zealand law (Section 11 of Wild Animal Control Act 1977).

Fig. 31.1 Phenotypic variation in male sika in New Zealand believed to reflect a mix of Manchurian and Japanese subspecies thought to have been present amongst the four or five founders of the population in 1905. (Photo credits: C. Speedy)

Within their ca. 9000 km^2 New Zealand range, sika are, or have been, widely sympatric with red deer (*Cervus elaphus*), but sika have largely displaced red deer from many parts of that range, possibly because of a foraging advantage (Fraser 1996). As in Britain and elsewhere, the two species hybridise, possibly initially as a result of initially rare mating that is followed by genetic introgression into both parental species as a result of backcrossing that is sometimes frequent and sometimes not (Senn and Pemberton 2009). In a recent Scottish study, it appeared that six to seven generations of such backcrossing had resulted in numerous 'hybrids' that are indistinguishable from one or the other of the parental stocks except through the use of genomic sequencing (McFarlane et al. 2020). In a 2017 sample of deer from the southern part of the New Zealand range, 28% were visually classified as hybrids (A Jackson, unpublished). Given the high percentage of phenotypically apparent hybrids, it would seem certain that many of the apparently 'pure' sika in that sample would also carry some red deer genes. Coupled with the unresolved uncertainty about the subspecific origins of the four or five founders, New Zealand 'sika' seem certain to be a globally unique form of the species.

31.2.2 History of Herd Development

The sika originally introduced were a gift to the New Zealand people (from the then Duke of Bedford) with the aim undoubtedly being to create a hunting resource—hunting was the sport of the upper classes in Britain, and the European colonists were keen to avail themselves of the same sporting opportunities (Banwell 2009). Sika were therefore initially fully protected. Although there are few records for two decades, the herd had clearly increased in number and range by 1925, when the first hunting licences were issued. Within a decade, the sika herd had become prized for its trophy value (Davidson 1973), possibly as much for their rarity value at that time as well as the 'prettiness' of the species. Sika have remained a sought-after trophy species for New Zealand hunters ever since, perhaps not only for antler quality and appearance but also for reasons of achievability during the latter third of the twentieth century (when red deer, by far the most common deer species in New Zealand,were greatly reduced in number by commercial hunting (Challies 1985).

The initial enthusiasm for introducing new species to New Zealand had already begun to wane by the time sika were introduced. European rabbits (*Oryctolagus cuniculus*), for example, were introduced in the 1830s but had reached plague proportions by the 1860s and outcompeted farmed livestock in some areas (Wodzicki 1950). Deer generally, and red deer in particular, likewise increased greatly in number and spread widely, again often competing with livestock for forage. By the early 1900s, deer were increasingly seen by farmers as agricultural pests. In addition, botanists and others feared deer would cause catastrophic dieback and collapse of native forests resulting in greatly increased erosion rates in the mountain lands that would threaten human populations and enterprises downstream (Cockayne 1928). Deer had emerged as an apparently serious threat to the economic and ecological well-being of the nascent nation. This culminated, in 1930, in a now famous national 'Deer Menace' Conference. Soon after that which all protection was removed from all deer species, including sika.

Over the ensuing three decades, there were widespread efforts to 'cull' (i.e. reduce) deer numbers, but generally there were too many deer and too little by way of budget (Caughley 1983). By the 1950s, over a hundred official deer cullers were killing 40,000–60,000 deer a year nationally (Challies 1985). Despite that, deer remained abundant in many areas, and deer hunting for sport, subsistence, and/or commercial reasons (such as the sale of skins) continued. Hunting became a recreational pastime for the common man with few restrictions on where and when one could hunt and how many animals could be taken. That egalitarian free-for-all ethos remains a hallmark of recreational hunting in New Zealand.

Like other deer, sika were subject to culling. In part of the Kaweka Range (the easternmost part of the sika distribution), official cullers operated for 204–1336 days p.a. during the 1958–1988 period, killing about one deer per day (Davidson and Fraser 1991). Initially, red deer dominated the cull (70–92% depending on the location within the targeted area), but by 1988, 70% of the deer shot were sika. The apparent displacement of red deer by sika was attributed to a combination of sika being more difficult to hunt than red deer (Kiddie, cited in Davidson and Fraser 1991); of red deer being the preferred target of commercial hunters (because of their larger body size); a preference for habitats with heavy shelter/escape cover; and a foraging advantage conferred by both their smaller body size and rumen morphology better suited to digesting poor forage (Fraser 1996).

In the late 1950s, commercial hunting (for the export of venison to Europe and elsewhere) began, with helicopters soon being used, initially to help recover carcasses from remote areas, but soon also as a shooting platform (Challies 1985). This focussed mainly on the larger-bodied red deer and by the mid-1970s had substantially reduced deer numbers in most of New Zealand, particularly in unforested areas with little cover (e.g. an 81% reduction in deer density in Fiordland; Nugent et al. 1987). The widespread decline in deer density as a result of commercial harvesting reduced the perceived need for government-funded deer culling. By the mid-1980s, broadscale culling had virtually ceased.

One curious side effect of the decline in deer numbers caused by the onslaught of commercial hunting was political pressure from recreational hunters for ‘protection’ of their sport—this led to the establishment of ten recreational hunting areas (RHAs) under the 1977 Wild Animal Control Act. Although the aim of deer management in these RHAs was ostensibly still to control deer numbers, commercial hunting was prohibited in them. Sika were to the fore with regard to RHAs, with two (Kaimanawa and Kaweka) of the ten established nationally being in the sika range. That outcome likely reflected both the high interest in sika by recreational hunters and, again, their lower value as a commercial resource.

The 1980s saw efforts to enhance the management of recreational hunting of sika, both as an activity in its own right (Fraser and Sweetapple 1992) and as a way of reducing sika impacts on the native vegetation (Speedy 1991). However, following the formation of the New Zealand Department of Conservation (DOC) in 1987 and its increased focus on protection of the indigenous biota, the RHA concept received little official support and, effectively, fell into abeyance. In a 2001 policy statement on deer management generally (Department of Conservation 2001), it was formally stated that ‘Deer are a serious conservation pest’ and further noted that active management of deer for the benefit of hunters was not to be encouraged because it risked management for higher deer densities that would detract from the goal of protecting the native biota. However, DOC still encouraged deer hunting through easy access to free year-round unlimited hunting in most areas. This usually simply involved providing hunters with legal permission to hunt on 8.5 million ha of public conservation land (32% of the country).

This ‘laissez-fare’ approach to the management of hunting (and therefore of management of deer) effectively aimed to maximise the hunting effort provided for free by recreational hunters. The implicit assumption was that maximising recreational hunting effort would reduce deer densities at least somewhat, which in turn would (hopefully) reduce their impacts on the native biota. There is some evidence to support that assumption. In the Kaimanawa Range (in the western part of the sika range), sika abundance was lowest in areas with the highest hunting pressure, with differences in hunting pressure determined mainly by differences in accessibility by road (Fraser and Sweetapple 1992). In areas easily accessible by road, deer densities were lower, the deer were bigger, and there tended to be more deer-palatable seedlings (Fraser and Speedy 1997).

In areas more than a few kilometres from a road, however, sika hunting is mostly limited to so-called fly-in-fly-out (FIFO) hunters who use helicopter transport to get to their hunting grounds. The high cost of such transport typically limits such hunters to just one FIFO hunting excursion per year, so hunting pressure in remote areas is low. It is also generally focussed on the rut period, when adult males are easiest to hunt, resulting in the FIFO harvest being heavily male biased. The consequence is that deer numbers in such areas are high and body size low. Reports of starving deer in the western Kaweka Range during the mid-1990s indicated that the deer there had exceeded their food supply (Nugent and Speedy 2021). One of us (C. Speedy) has recorded eviscerated carcass weights for adult sika females of just 15 kg in such areas compared to a previously recorded average of 31.0 kg (Nugent and Speedy 2021).

Where sika densities are near carrying capacity (which is believed to often be well in excess of 15 deer/km^2; Nugent and Speedy 2021), the consequence is high browsing pressure on seedlings and saplings of the main canopy species, resulting in non-replacement of the forest canopy in some parts of the worst affected areas, particularly at forest margins (Allen and Allan 1997). The severity of that impact was attributed not only to limited control but also to a greater impact of sika relative to red deer because of a presumed better ability to digest poor forage (Husheer et al. 2006). It is likely exacerbated by the tendency for sika to favour ecotones between forested and open areas (Latham et al. 2015). That threat to full canopy replacement prompted a return of culling (in the form of helicopter-based shooting to waste) in part of the Kaweka Range, which rapidly reduced deer density there from 16 per km^2 in 1998 to 6 per km^2 in 2001 (Husheer and Robertson 2005). In total, >4700 deer were removed from a 267 km^2 area between 1998 and 2015, reducing faecal-pellet counts by >50% and improving deer condition and reproductive rates (Mayo, cited in Nugent and Speedy 2021). The culling operation has now ceased.

Currently, recreational hunting is the only factor limiting sika numbers and impact and in many areas has only moderate or little effect. As a result, sika densities tend to be high by New Zealand standards, as illustrated by a recent estimate of

20 deer per km^2 in the north-eastern Kaimanawa Mountains in 2017 (G. Morriss and G. Nugent, unpublished) compared to an estimated average of just 4 deer/km for the entire New Zealand deer range (Nugent and Fraser 1993).

31.3 Sika as Conservation Pests

For over 80 years following the famous ‘Deer Menace’ Conference in 1930 (i.e. until the Game Animal Council (GAC) Act of 1913), the only legal status of wild deer in New Zealand was effectively as pests. There was arguably some recognition of recreational hunting as a legitimate pursuit in the 1977 law that allowed for the creation of RHAs, but even within RHAs recreational hunting was, ostensibly at least, to be managed as a deer control tool rather than for hunting benefits per se.

Many of the original justifications for classing deer as pests have now been largely debunked, perhaps most eruditely and forcefully by Caughley (1983). Focussing specifically on sika, they have never been seen as a major economic threat to agricultural production, as most of their range is unfarmed forest and mountain-land. Indeed for some private landowners within the sika range, sika provide a substantial revenue source (through the sale of hunting rights).

The original conservation concern, in the early 1900s, was most famously espoused by a pre-eminent botanist of the time (Cockayne 1928). He posited that New Zealand’s native flora was inherently extremely vulnerable to browsing by introduced mammalian herbivores simply because it had evolved in the complete absence of such browsers. However, prehistoric New Zealand did not lack for browsers. A suite of flightless bird species (most notably nine species of moa (Dinornithiformes)) was present until about 600–700 year ago, all of them herbivores, and some of them extremely large, with the largest weighing up to 249 kg (Szabo 2013). A recent estimate suggests densities of between 2 and 10 moa/km^2, with a medium-density prediction of 4/km^2 (Latham et al. 2020), much the same as the estimated nationwide average density for deer in the late 1980s (albeit after they had been reduced by commercial hunting) (Nugent and Fraser 1993). Macrofossil and DNA-based investigations of moa diet indicate that some moa were generalist herbivores (Wood et al. 2020). It therefore seems certain that the native flora would have developed various forms of resistance to moa browsing, with the widespread evolution of a divaricate (small-leaved and wide-angled multi-branched) growth form in New Zealand plants—most strikingly in the juvenile growth forms of taller trees until they exceed 3 meters in height (the probable maximum reach of the largest moa)—hypothesised to be an example of that (Greenwood and Atkinson 1977).

Although it is strongly argued by some that deer cannot be viewed as close surrogates for the now extinct moa (Wood et al. 2020), defences such as divarication do confer some degree of protection from deer, at least in less benign climates (Lusk et al. 2020). More broadly, it is now clear that while many New Zealand plants species are highly palatable to deer, many others are not (Forsyth et al. 2002; Forsyth et al. 2005). A crucial characteristic of current deer diet in New Zealand forests is

Fig. 31.2 New Zealand sika in native forest habitat showing some of their phenotypic diversity but mainly emphasising the 'eaten-out' understorey in which deer glean fallen (mostly yellowed) leaves of preferred broad-leaved subcanopy tree species. The abundant mosses and ferns in the picture are highly unpalatable. The hard-antlered stag shows the low trophy quality typical of eaten-out areas—it was subsequently shot and was estimated to be 7 years old with weight of just 25 kg (C. Speedy, unpublished data). (Photo credits: Manaaki Whenua–Landcare Research trail cameras)

that deer generally rely heavily on the fallen leaves of highly preferred broad-leaved subcanopy tree species (Nugent and Challies 1988; Nugent 1990) that established before deer were introduced or which have recently established as epiphytes or on steep banks and bluffs out of direct reach of deer. The same is true of sika (Fraser 1991) (Fig.31.2). One consequence of that is a significant part of the deer food supply (in the short term) remains largely unaffected by current deer density, so deer numbers can remain high even when the biomass of preferred foods actually growing within direct reach of deer has been driven to near zero (Nugent et al. 2001). While the adult trees of a few New Zealand species can be killed as a result of ring-barking by deer (Mark and Baylis 1982), those species are rare in the sika range, so the main effect of deer browsing in forests is the elimination of seedlings of preferred tree species. The result is that regeneration of those preferred tree species within (and eventually through) the browse tier would require deer numbers to be reduced to very low levels for prolonged periods.

Fortunately, as a generality a majority of canopy-forming species in New Zealand tend to be avoided rather than preferred by deer (Forsyth et al. 2002), and, also as a broad generality, less palatable species tend to increase in abundance, while palatable species decline when deer densities are high (Augustine and McNaughton

1998). The prevention of mountain beech (*Fuscospora cliffortioides*) canopy regeneration in part of the sika range mentioned above is therefore something of an exception, with the tendency for mountain beech to occur at the harshest extremes of forest cover as a low-diversity forest type coupled with the ability of sika to survive on a poor diet probably being the key contributing factors. Overall, however, the impacts of deer tend therefore to be one of compositional change rather than catastrophic collapse, particularly in less fertile situations (Forsyth et al. 2015), such as the volcanic pumice and ash soils of the Central North Island sika range.

The key question is whether those impacts are important threats to the conservation of indigenous biodiversity. The answer depends in part on how serious a threat sika pose to the native forests they now inhabit, compared to the risks posed by other threats. DOC has adopted a place-based approach to classifying areas according to their conservation value (https://www.doc.govt.nz/globalassets/docum-ents/about-doc/role/managing-conservation/setting-priorities-factsheet.pdf. Accessed 16 March 2021) and has identified 850 areas of greatest conservation value. These areas are given priority for protective action against pests and other threats. The sika range contains very few of those most valued sites and none of the highest-ranking sites. Perhaps as a consequence, the helicopter-based culling of sika aimed at allowing canopy regeneration in part of the Kaweka Range mentioned above ceased in 2017. More broadly, nationwide, there are now only three places where established deer populations are subject to government-funded control programmes (D. Carlton, personal communication), compared to a many tens or even hundreds of other public and private programmes currently focussed on the much more immediate impact of a suite of introduced small mammal 'predators' such as mustelids, rodents, and possums (*Trichosurus vulpecula*) that are driving some native bird species towards extinction (Elliott and Kemp 2016). The harsh reality then is that although sika are driving major changes in ecosystem composition and structure, that impact is currently seen as less urgent than the plethora of more important and urgent conservation threats and risks elsewhere.

31.4 Sika as a Hunting Resource

Recreational hunter interest in sika deer hunting has long been high, as indicated by two 'sika' RHAs (Kaimanawa and Kaweka) being formally declared in the 1980s. In 1988, around 6000 ground-based (mostly recreational) hunters harvested an estimated 6900 sika deer, and a further 1000 were shot commercially. That equated to a harvest rate of <1 deer per km^2 which is very low when compared with the density estimates cited above.

The ongoing popularity of sika is perhaps best shown by a national survey in 2011/2012 in which 31% of 1251 big game hunters reported hunting sika (Kerr and Abell 2014). It is also shown by the high number of hunting permits issued (by DOC) to hunt in the two main areas of publicly owned land within the sika range (the Kaimanawa and Kaweka Forest Parks, combined total area: 1453 km^2)—

in 2016, 14,169 such permits were issued for those two parks, almost 10/km^2. That compares with an average of just 3.1/km^2 nationwide (252,665 permits issued in 2016 for 81,382 km^2 of public conservation land).

The high interest (relative to the area of New Zealand deer range occupied by sika) undoubtedly partly reflects the higher-than-average densities of sika deer over the last five to six decades that largely resulted from their being a less commercially attractive target than red deer. Commercial hunters selectively target the largest animals available simply because they provide greater monetary returns (Challies 1985), so the effect of such hunting on suppressing deer density has inevitably been far greater for red deer than for sika, particularly for large-bodied males. The resulting higher densities of sika males are obviously associated with longer average lifespans and greater availability of mature males that makes the sika population especially attractive to trophy hunters (Kerr and Abell 2016). The sale of hunting access rights also provides some private landowners with substantial revenue. Another measure of sika popularity is the annual ‘Sika Show’, which has become one of the largest outdoor recreation trade shows in New Zealand.

Under current sika management on public land, hunting is officially encouraged, not in its own right but effectively in the hope, largely (we believe) in vain, that it will hold deer numbers and their unwanted impacts a little lower than they would otherwise be. That approach has some conservation benefits where hunting pressure is highest (i.e. where access is easy), but that is not the case for large parts of the sika range. The consequence is that sika numbers in those remote areas are high and sometimes close to carrying capacity. Their impacts on the ecosystem in such places are at their most extreme, and the animals are in poor condition, resulting in minimal meat yields and low trophy value (Fig.31.2). The harsh reality for hunters is that unlimited open-access hunting does not automatically maximise the overall value of the hunting resource. It tends to result in either very high hunting pressure where access is easy, making hunting difficult and less safe (with success rates below low and almost no males reaching adult (trophy) size), or low hunting pressure with more or less opposite outcomes.

31.5 Future Management

At present, the laissez-faire management of sika is arguably more of a lose-lose situation than the hoped-for win-win of high numbers of hunters happily maintaining low densities of deer that have little impact on the native forests they inhabit. That outcome is perhaps achieved to some extent in the immediate vicinity of roadways, but for the bulk of the sika range, hunting pressure is much lower (and hugely male-focussed), and sika densities are high. With densities in some places close to or at carrying capacity, impacts on native plants are at their highest, while for hunters, deer body size is small (resulting in a low meat yield), and trophy quality is low.

Could more active management of recreational hunting produce better outcomes? Conservation funding appears likely to remain strongly focussed on the higher priority areas and threats outside the sika range. The need, therefore, is to determine whether more active management of sika could result in better outcomes for conservationists and for hunters. The Central North Island Sika Foundation was established in 2015, with the specific aim of having the main sika herd designated as a Herd of Special Interest under the Game Animal Council Act 2013 of New Zealand. That would enable parts of the sika range to be managed for hunting benefits within environmental constraints. A formal proposal for that has been developed. The key features are (1) the adoption of different objectives in different parts of the sika range, with objectives ranging from trophy enhancement through to culling for canopy protection; (2) a focus on encouraging recreational hunters to harvest increased numbers of females (something many are currently unmotivated to do); and (3) hunter-funded reductions of deer numbers (culling) where conservation threats are highest. While the outcome of the proposal is yet to be decided, the concept seems to offer the potential for better outcomes for both conservationists and hunters (and sika, if starving subpopulations are considered undesirable).

In summary, sika in New Zealand are a globally unique species, which despite (or because of) their genetically mixed origins have thrived in New Zealand and become a major hunting resource. That partly reflects their continued relative (geographical) rarity in New Zealand, higher trophy potential, and overall 'daintiness' (compared to more 'angular' and ubiquitous red deer). It also reflects their well-recognised ability to thrive in poor habitat, but that same ability also makes them arguably a greater potential threat to conservation goals than other deer species. Unfortunately, that has placed them at the forefront of the entrenched conflict between hunters and conservationists. That long-standing conflict has resulted in a lack of active management that currently delivers suboptimal outcomes for both groups. The challenge now is to determine whether more active management can do better. The biggest impediment appears to be a reluctance by at least some in the broader conservation movement to compromise—they appear to fear (as per the official policy of 2001; Department of Conservation 2001) that allowing deer to be managed for hunting benefit in some places will result in the development of deer management systems focussed on maximising deer harvest. However, with the decline of commercial hunting in New Zealand (which never greatly affected sika anyway) and the broader societal decline in interest in recreational hunting globally (Price Tack et al. 2018; Hansson-Forman et al. 2020), the issue is increasingly one of encouraging hunting generally.

It is interesting to speculate on the effect of current and potential future management systems on the evolution of sika in New Zealand. It is likely that even the most sika-like animals in the population have some mixture of genes from two or more sika subspecies and from red deer. The widely accepted ability of sika to outcompete red deer in areas where deer-habitat quality is generally low suggests that sika phenotypes (foraging and otherwise) will be strongly selected for in such areas, whereas in habitat more favourable to red deer, hybridisation will likely continue, and hybrid phenotypes may be favoured. At the margins, suspected ongoing introgression of sika into red deer range will continue to create cryptic red deerlike hybrids.

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Part VI
Towards Science-Based Management

Chapter 32
Adaptive Management of Sika Deer Populations on Hokkaido Island, Japan

Hiroyuki Uno, Yoshihiro Inatomi, Mayumi Ueno, and Koichi Kaji

Abstract We review the management policy and practice for sika deer (*Cervus nippon*) on Hokkaido Island, the northernmost in Japan. We introduce the population management and damage management between 1993 and 2018 in the three districts, the East, the West, and the South of the island based on the Conservation and Management Plan for Sika Deer. The population estimates peaked at 2011 in the East and the West, and then they have decreased because of population control by the prefectural government. The estimated population size in 2018 was 330,000 (95% credible interval: 250,000–470,000) in the East, and it was 380,000 (250,000–620,000) in the West. The overabundance of sika deer populations severely influenced the local ecosystems, especially the forest vegetation. We describe the two case studies of ecosystem management, one in the Akan-Mashu National Park and the other in Shiretoko National Park. We discuss the importance of hunting system for resource management and that of culling system for ecosystem management.

32.1 Introduction

Hokkaido is the northernmost island in the Japanese Archipelago and occupies an area of 78,421 km^2; approximately 70% of this area is covered by forests. The island is surrounded by the Pacific Ocean, the Sea of Japan, and the Sea of Okhotsk; the

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H. Uno (✉)
Faculty of Agriculture, Tokyo University of Agriculture and Technology, Fuchu, Japan
e-mail: unoh@go.tuat.ac.jp

Y. Inatomi · M. Ueno
Research Institute of Energy, Environment and Geology, Hokkaido Research Organization, Sapporo, Japan
e-mail: inatomi@hro.or.jp; jmayueno@hro.or.jp

K. Kaji
Tokyo University of Agriculture and Technology (Retired), Fuchu, Japan
e-mail: kkaji@cc.tuat.ac.jp

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Tsushima Warm Current flows westward, and the Kuril Cold Current flows eastward in Hokkaido. The mean annual temperature is 5–10 °C, annual precipitation is approximately 1200 mm, and annual snow accumulation is approximately 30 cm in the southeast and approximately 240 cm in the west. The difference in snow depth between the East and West affects the pattern of sika deer (*Cervus nippon*) distribution. The exploitation of deer for meat, fur, and antler as well as heavy snow substantially reduced deer populations by the end of the nineteenth century (Uno et al. 2009). The predator of sika deer, gray wolf (*Canis lupus*), extincted in the 1890s, because humans killed them to protect their livestock from predation (Inukai 1933; Walker 2009). Hunting of deer was banned twice, from 1889 to 1899 and from 1920 to 1956, as the harvest of deer had decreased in the 1880s and 1910s (Inukai 1952). After a decrease in the genetic diversity of sika deer during this period, three major populations have survived the bottleneck in the Akan, Hidaka, and Daisetsu mountain regions (Nagata et al. 1998; Kaji et al. 2000). These three groups were genetically recognized as haplotypes of mitochondrial DNA (Nagata et al. 1998). During the Second World War (1939–1945), deer populations gradually recovered. The replacement of native hardwood forests with conifer plantations and pasture acreage may have contributed to the recovery of deer distribution and abundance (Kaneko et al. 1998).

32.2 Distribution and Current Status

Sika deer occupied the available habitats in the eastern half of Hokkaido by the mid-1970s and had spread to the western part of the island by the 1990s (Kaji et al. 2000). Furthermore, the distribution has expanded to the southern part of the Oshima Peninsula and has occupied the entire habitats in the 2000s. On the contrary, eight and nine deer were introduced to the Oshima Peninsula from eastern Hokkaido in 1980 and 1981, respectively (Kaji et al. 2006). Terada et al. (2013) found new mitochondrial DNA haplotypes in this area and suggested human-mediated immigration, and this raised the concern of genetic contamination.

The number of registered hunters in the Hokkaido Prefectural Government peaked at 20,620 in 1978 and decreased to less than 10,000 in 2004 and 8205 in 2018 (Fig. 32.1) (Hokkaido Government, unpublished data). Figure 32.1 shows the number of deer harvested from 1957 to 2018 in Hokkaido. Bucks-only hunting was allowed from 1957 to 1993, and female hunting was allowed in 1994. Nuisance culling is permitted by the prefectural governments in Japan (Table 32.1). Municipalities (and/or agricultural cooperative associations) execute deer culling to reduce crop damage. The Hokkaido Prefectural Government has started female culling from 1980 after an increase in crop damage. The upper limit of deer culling was only two deer (one male and one female) per culler-day in 1980–1996; however, it eased to 1200 deer per permission in 1997 (Uno 2017).

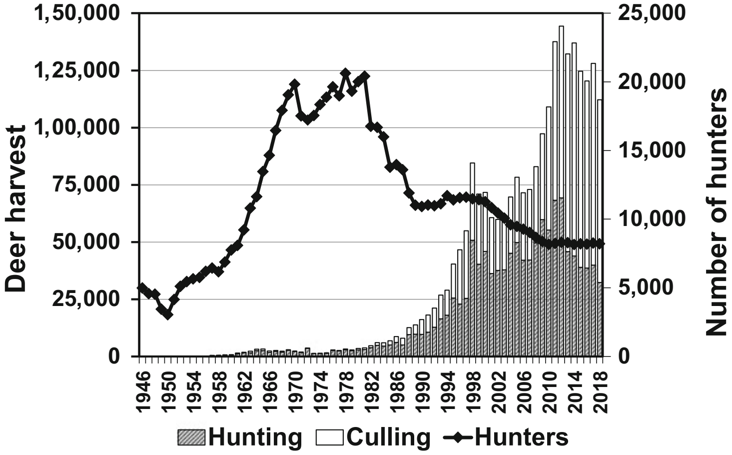


Fig. 32.1 Changes in sika deer harvest and the number of hunters in Hokkaido. The shaded bars indicate the number of sika deer harvested by hunting, the white bars indicate that by culling, and the black line indicates the number of sport hunters registrated to Hokkaido Prefectural Government. (Data from Hokkaido Prefectural Government, unpublished)

Table 32.1 Deer management structure in Japan

Organizations	Role
Ministry of the Environment	Responsible for the Wildlife Protection and Hunting Management Law
Ministry of Agriculture, Forestry and Fisheries	Responsible for the Wildlife Damage Special Measures Act
Prefecture	Set management plans Set hunting regulations Permit nuisance culling (control kill) Monitor population trends
Municipality	Set local goals Execute nuisance culling (control kill)

32.3 Population Management

Games are regarded as *res nullius* in Japan. The Ministry of the Environment enacted the Wildlife Protection and Hunting Management Law, and the prefectural governments set management plans based on it (Table 32.1). In addition, firearms are controlled under the National Police Agency.

The Hokkaido Government established the Conservation and Management Plan for Sika Deer (CMPS) in 1998 and proposed that management based on sex-specific hunting was effective in diminishing the annual variation in hunting yield (Hokkaido Government 1998; Matsuda et al. 1999). Its goals are as follows: (1) to prevent population irruption and related severe damage to agriculture and forestry, (2) to avoid the risk of deer extinction, and (3) to maintain a sustainable yield of deer. The

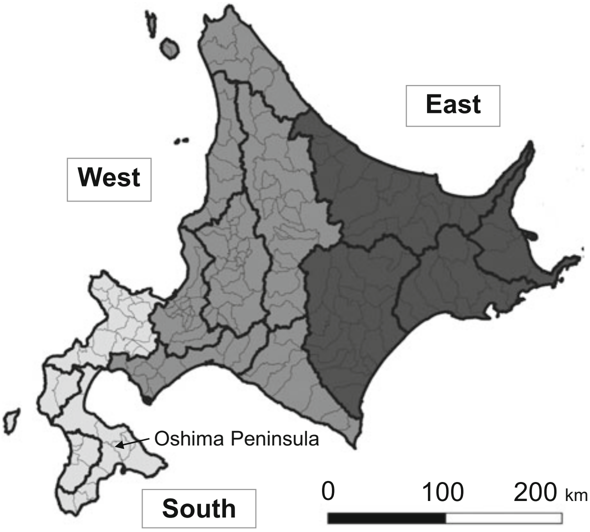


Fig. 32.2 The three districts in the Conservation and Management Plan for Sika deer (Hokkaido Government 2008). Bold lines denote the boundaries of sub-prefecture, and thin lines denote municipalities

aim of reducing ecosystem impact was added to the three goals mentioned above in the 2002 CMPS (Hokkaido Government 2002). Fourteen sub-prefectures (SPs) were divided into three management districts: the East (four SPs, with an area of approximately 31,060 km^2), the West (seven SPs, 36,531 km^2), and the South (three SPs, 10,872 km^2) (Fig. 32.2). We considered three levels of relative population sizes (irruption, optimal, and critical level) and four management programs (emergent decrease, gradual decrease, gradual increase actions, and ban on hunting) and chose one of the four actions based on the estimates of population size indices (Matsuda et al. 1999). This management concept is called “feedback management” which was referred to as the revised management procedure by Tanaka (1982).

32.3.1 Population Trends

We used five population size indices, namely, the spotlight count, sighting per unit effort (SPUE), catch per unit effort (CPUE), aerial count, and damage value to agriculture and forestry (Kaji et al. 1998; Uno et al. 2006). We evaluated these five indices and concluded that spotlight count was the most useful index because it was less subject to artificial biases than the others and showed consistency (Uno et al. 2006). However, the spotlight index did lead to an underestimation; for example, in 1994, the SPUE index was effective in checking the validity of the spotlight index (Uno et al. 2006).

We established 61 fixed survey routes in the East in 1992 (Kaji and Tomizawa 1993) and conducted annual deer spotlight counts from 1992 to 2018 between late October and early November. We used a vehicle driven at a speed of 20–40 km/h on each fixed route; each route was approximately 10-km long. We calculated the

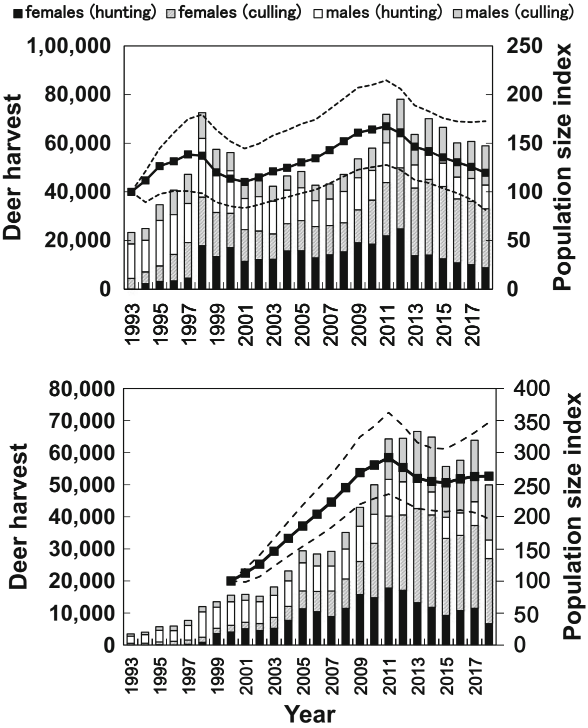


Fig. 32.3 Bayesian estimates of population size indices that were obtained from the state-space model based on the stage-structured model (Yamamura et al. 2008) and the number of deer harvest from 1993 to 2018. (**a**) In the eastern part and (**b**) in the western part of Hokkaido, bold lines denote the estimates of population size indices; dotted lines denote *SE*

number of deer observed per 10 km as the spotlight index (Uno et al. 2006). The number of fixed routes was 61 in the East at the beginning; 157 in the East, West, and South in 2005; and 207 in all municipalities (excluding those in isolated islands) from 2011 to 2018.

The population trends estimated using the state-space model with the expected value of spotlight count by GLMM and harvest data (Yamamura et al. 2008) are shown in Fig. 32.3. The population size in the East increased to 138% in 1997 compared with that in 1993 and then decreased to 110% in 2001 due to population control based on the CMPS (Fig. 32.3a). Thereafter, it increased to 167% in 2011. Since the Ministry of Agriculture, Forestry and Fisheries established the Act on Special Measures for Prevention of Damage Related to Agriculture, Forestry and Fisheries Caused by Wildlife (Wildlife Damage Special Measures Act) in 2006 and subsidized the cost of culling to municipalities (Table 32.1), 78,076 deer (28,208 males and 43,863 females) were harvested in 2012. The population size in the East then decreased from 160% in 2012 to 120% in 2018 due to aggressive culling (Fig. 32.3a). Contrarily, the population size in the West consistently increased to 292% in 2011 compared with that in 2000 because of a low capture pressure (Fig. 32.3b). Because 64,305 deer (24,059 males and 40,246 females) and 64,533 deer (23,939 males and 40,594 females) were harvested in 2011 and 2012, respectively, the population size declined in 2012 (Fig. 32.3b).

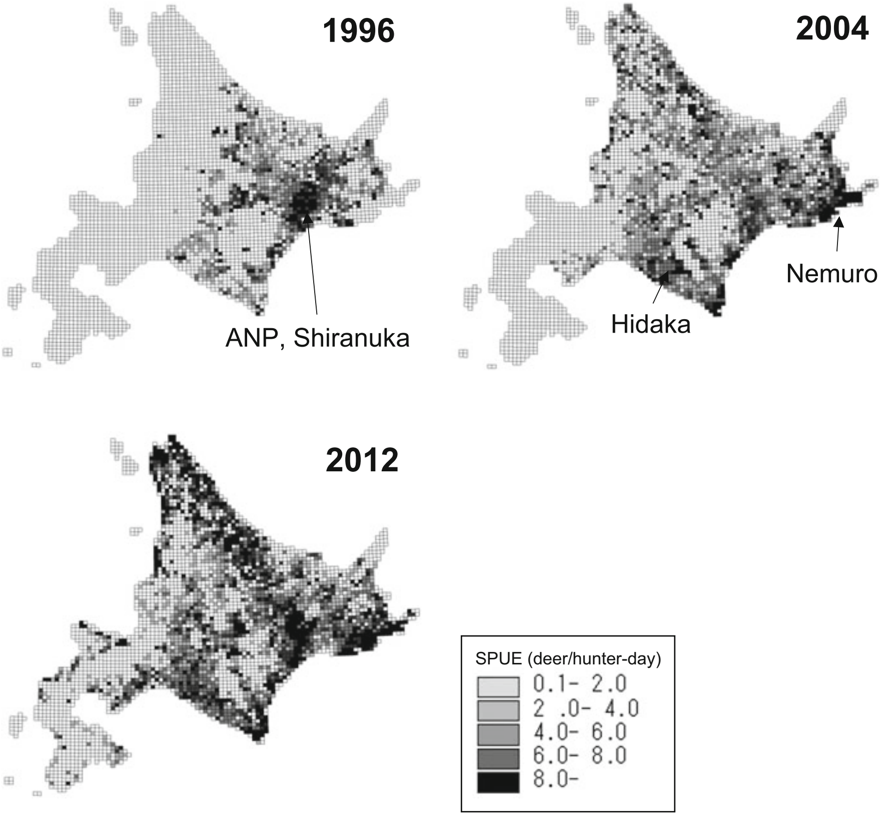


Fig. 32.4 Changes in the number of deer sighted per hunter-day, SPUE index (Uno 2017). Each block is about 5 × 4.6 km

We collected the records of hunter activities (i.e., number of deer killed or observed per hunter) from questionnaire surveys and used these data to estimate the CPUE (catch per unit effort) and SPUE (sighting per unit effort) (Uno et al. 2009). We analyzed 31,835, 64,531, and 57,790 data points in 1996, 2004, and 2012, respectively, and the results are shown in Fig. 32.4 (Uno 2017). The high deer density area where the SPUE index was more than 8.0 deer per hunter-day concentrated in Kushiro (including Akan-Mashu National Park and Shiranuka Hills, Uno et al. 2009) in 1996 and expanded in Hidaka and Nemuro in 2004 and throughout the East and West districts (excluding the South) in 2012 (Fig. 32.4).

32.3.2 Estimation of Population Size

The deer population in the East in 1993 was first estimated to be between 74,000 and 166,000 (90% confidence interval) using aerial surveys (Hokkaido Institute of Environmental Sciences 1995). The harvest exceeded the estimated natural population increase during the first several years under the emergent decrease action of the CMPS, assuming an annual rate of increase of 16%–21% (Kaji et al. 2004). However, the population size indices were higher than those expected; therefore, we suspected that the 1993 population size had been underestimated.

Matsuda et al. (2002) proposed a harvest-based estimation of population size, which requires information about actual trends in relative density indices, the rate of natural increase, and the number of animals (males and females) harvested. In this method, the total number of individuals is estimated by examining the response of the population index to a known number of individuals that have been artificially removed. Using a stage-structured matrix model and feasible sets of parameter values in the resultant simulations for the population, we re-estimated the 1993 population size to be between 170,000 and 330,000 in the East (Matsuda et al. 2002).

Using harvest-based estimation, we were able to obtain more reliable estimates of population size. However, the uncertainty in the estimation of the absolute population size was still large. It is well known that estimates using indices suffer from large observation errors when the probability of observation fluctuates widely. In fact, there was an unexplained temporal decline in the spotlight index from 1993 to 1994 (Uno et al. 2006). Therefore, we applied state-space modeling to harvest-based estimations to consider observation errors (Yamamura et al. 2008). We also proposed the use of Bayesian estimation with uniform prior distributions as an approximation of the maximum likelihood estimation. Using these models, the 2018 population size was estimated to be a median of 330,000 (95% credible interval: 280,000–470,000) in the East and 380,000 (250,000–620,000) in the West (Table 32.2; M. Ueno et al. unpublished

Table 32.2 Summary of estimated population size, number of sika deer harvest, damage value, and population status in the three management districts of Hokkaido, 2018

Districts	Estimated population size (95% credible interval)	Deer harvest[a]		Damage value to agriculture and forestry[a] (million yen)	Population status
		Hunting	Culling		
East	330,000[b] (280,000–470,000)	18,532	40,392	2,524	Decreasing
West	380,000[b] (250,000–620,000)	12,441	37,533	1,232	Stable, but a slight increase
South	Unknown (30,000–130,000)	1,328	2,006	102	Increasing

[a] Hokkaido Government unpublished data

[b] Population size was estimated according to the state-space model of Yamamura et al. (2008)

data). We could not sufficiently estimate the population size in the South using the harvest-based model.

32.4 Damage Management

32.4.1 Damage to Agriculture and Forestry

The cost of agricultural and forest damage increased in the 1980s and 1990s, reaching 5 billion Japanese yen in 1996 (Uno et al. 2009). Thereafter, it decreased from 1996 to 2004 because 2.5 m net fences were erected to exclude deer from agricultural fields. The decrease in population size in the East also contributed to reduced crop damage. The total length of extending fences was approximately 1209 km in 1998 and 3010 km in 2003 (Kaji et al. 2006). Moreover, its total length has exceeded 8000 km in 2014 (Hokkaido Development Engineering Center and Yezo Deer Association 2015). In addition, chemical repellents such as ziram (dimethyldithiocarbamate) have been sprayed to reduce deer browsing of conifer trees (*Abies sachalinensis* and *Larix kaempferi*) (Uno et al. 2009). Net fences have also been established around the plantations of these species to protect nursery trees. The damage value in the East was 4.1 billion Japanese yen in 2012, and it decreased to 2.5 billion in 2018; the damage value in the West was 2.3 billion yen in 2011 and decreased to 1.2 billion yen in 2018 (Fig. 32.5, Table 32.2). The main issue in reducing damage is the deterioration and maintenance of net fences in recent years (Inatomi et al. 2013).

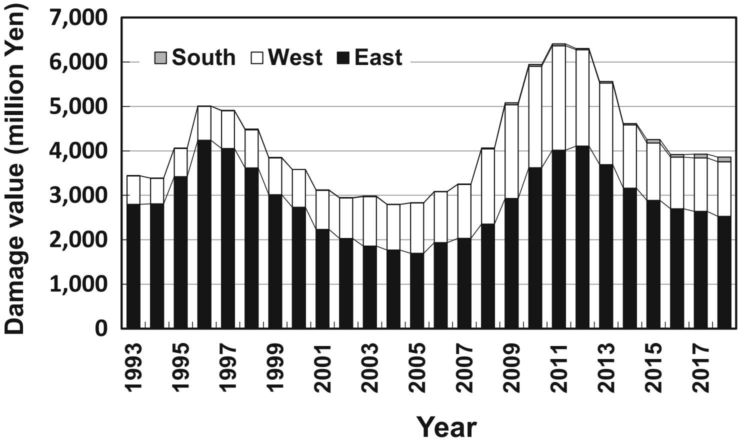


Fig. 32.5 Changes in the amount damage value to agriculture and forestry (Data from Hokkaido Prefectural Government). The management districts (East, West, and South) are shown in Fig. 32.2

32.4.2 Traffic Accidents

Deer-vehicle collisions are common. In 2008 and 2018, 1628 and 2834 road kills were recorded, respectively (Hokkaido Government 2020). Most of the collisions between deer and vehicle occurred during the autumn season (October and November). Deer-train collisions are also a common event. Two hundred and eighty-five rail kills (204 in the East, 80 in the West, and 1 in the South) were recorded in 1993, and it increased to 2750 (1005, 1441, and 304, respectively) in 2018 (Inatomi 2021). These collisions cause significant economic losses.

32.5 Impact on Ecosystem

The irruption of sika deer in the Akan-Mashu National Park (ANP) severely affected both overstory and understory forest vegetations (Uno et al. 2009). The survival and growth of tree seedlings are affected by deer browsing in ANP (Uno et al. 2019). Deer irruption behavior has also been reported on Nakanoshima Island in Lake Toya and Cape Shiretoko in the Shiretoko National Park (SNP) (Kaji et al. 2009). Debarking and foraging by deer have changed forest composition and coastal vegetation communities on Cape Shiretoko (Kaji et al. 2009; Ishinazaka 2016), affecting the changes in bird and insect populations (Tamada 2007; Ozaki et al. 2013).

Sika deer have also influenced wetland vegetation (bogs, fens, and swamp forests) in the Kushiro-Shitsugen (mire) National Park (KNP) (Fujita et al. 2012; Inatomi et al. 2018). The length of deer trails in the mire increased by more than two times from 1977 to 2004, and deer grazing and trampling created a new plant community near the bare ground (Fujita et al. 2012). For ecosystem management, nuisance culling was started in 2004 in the ANP, in 2007 in the SNP, and in 2013 in the KNP.

32.5.1 Akan-Mashu National Park

The ANP is located in the eastern part of Hokkaido (Fig. 32.6), occupies 904 km^2, and is comprised of mixed forests with coniferous and deciduous broadleaved trees. Mt. Meakan (1499 m a.s.l.), Mt. Oakan (1371 m), Mt. Mashu (857 m), and crater lakes (Lake Akan, Kussharo, and Mashu) are the main landscape features. Deer migrate a distance of 2.5–42.0 km from wintering area in the ANP to their summer habitat (mainly outside the ANP) (Uno and Kaji 2000).

The population size in and near the ANP increased in the 1980s (Uno 1991; Kondo et al. 1994), and bark stripping of trees was considerable in the 1990s in the ANP (Kondo et al. 1994; Uno et al. 1998). We conducted aerial surveys of native

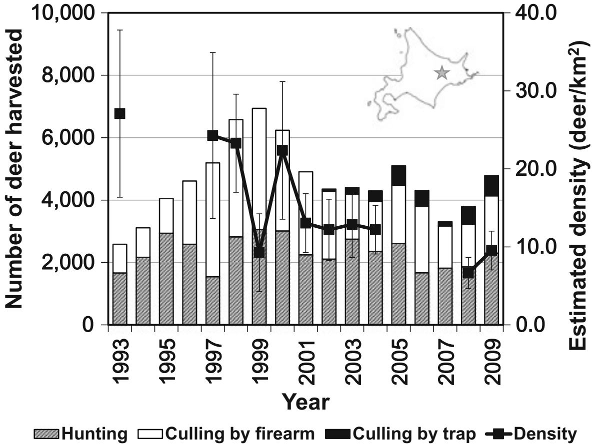
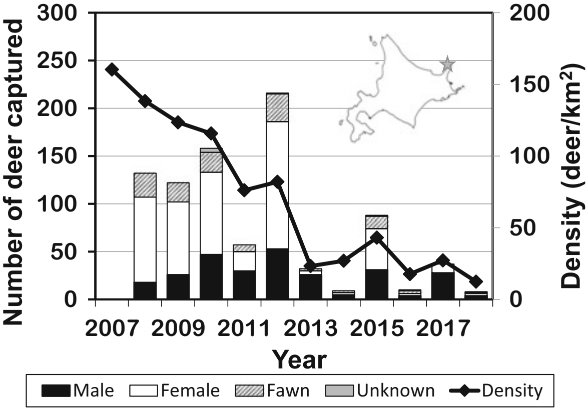


Fig. 32.6 Changes in the number of sika deer harvested and the deer density estimated via aerial survey in the Akan and Kushiro Districts in 1993–2009. The shaded bars indicate the number of deer harvested by hunting, the white bars indicate that by culling using gun, the black bars indicate that by culling using corral traps, and the black squares and line indicate the estimated density (deer/km^2) via aerial counts. Error bars indicate *SE*

forests of 87.1 km^2 around Lake Akan, which is a major wintering area; the estimated deer density decreased from 27.1 ± 10.7 deer/km^2 (mean ± *SE*) in 1993 to 9.5 ± 2.5 in 2009 by intensive culling (Fig. 32.6; Uno et al. 2006; Inatomi et al. 2012). The Hokkaido Government allowed female deer hunting in 1994, near the ANP. Annually 2272–3312 female deer were harvested by hunting every 10 days from 1994 to 1996 in 10 municipalities near the ANP. Nuisance culling via firearms was performed in the pastureland outside the ANP to reduce crop damage, and 139–607 deer were removed annually using corral traps to reduce the effect on forest vegetation in the ANP in 2002–2009 (Fig. 32.6; Niida 2011). Female hunting and culling in and near the ANP successfully decreased deer density below 10 deer/km^2 (Inatomi et al. 2012).

We surveyed understory plants in deer-excluded and control-unfenced sites between 1995 and 2010 and found that the cover and/or height of palatable plants (e.g., *Sasa senanensis*, *Thalictrum* spp., and *Trillium* spp.) increased, and an unpalatable plant (*Senecio cannabifolius*) disappeared simultaneously with a decrease in deer density (Inatomi et al. 2012). We also surveyed the tagged tree seedlings in the same sites between 2009 and 2011 and found that the browsing pressure of deer was still high for their survival and growth and suggested that the recruitment was limited to broad-leaved tree populations (Uno et al. 2019).

Fig. 32.7 Changes in the number of deer removed and the deer counts via aerial survey on Cape Shiretoko in 2007–2018. (Modified from Ishinazaka 2016 and the Ministry of the Environment unpublished data)



32.5.2 *Shiretoko National Park*

The SNP is located in the Shiretoko Peninsula, northeastern Hokkaido (Fig. 32.7), and occupies an area of 610 km^2. The Shiretoko Peninsula is surrounded by the Sea of Okhotsk and the Nemuro Strait. It was designated as a World Natural Heritage Site (WNHS) (487 km^2 terrestrial and 224 km^2 coastal area) in 2005 based on the following two criteria: ecosystems and biodiversity (Uno 2016).

The deer population in the SNP increased in the late 1980s. The number of deer observed in aerial surveys was 54 (11 deer/km^2) in 1986 and 592 (118 deer/km^2) in 1998, and the population crashed in 1999 (Kaji et al. 2004). In 2003, it recovered to 626 (125 deer/km^2) and re-crashed in 2004 (Kaji et al. 2010). Thereafter, deer density continued to increase, and foraging pressure degraded coastal and forest vegetations. The CMPS in the Shiretoko Peninsula was framed in 2006. The objective of the plan is to reduce the effects of deer overabundance on the ecosystem, following an approach that supports natural regulation but also allows active management intervention (e.g., culling and protection of vegetation using net fences) if risks to endangered species or endemic plant communities become too high (Uno 2016). Our approach to manage these impacts in the SNP has been to monitor the population dynamics of deer and the process of vegetation recovery and to better understand the ecological processes. We started culling as a manipulation on Cape Shiretoko in December 2007, and 869 deer (272 males, 466 females, 123 fawns, and 8 unknown) were removed from 2007 to 2018 based on the plan (Fig. 32.7; Ministry of the Environment, unpublished data). As a result, the number of deer observed by aerial survey decreased to 75 (23.2 deer/km^2) in 2013 and 40 (12.4 deer/km^2) in 2018 (Ishinazaka 2016; Ministry of the Environment, unpublished data). Currently, we are monitoring how vegetation restore, according to measurement of cover and height of plant species for decades as an indicator (Ishinazaka 2017).

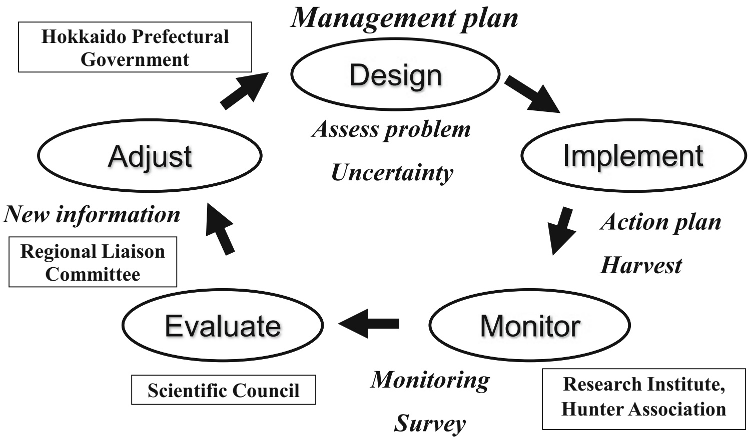


Fig. 32.8 The framework of an adaptive management for sika deer in Hokkaido. (Modified from Kaji et al. 2006)

32.6 Consensus Building and Decision-Making

The Hokkaido Government established the Hokkaido Institute of Environmental Sciences (HIES) in 1991 and started monitoring the sika deer population using population size indices. This was the beginning of a more scientific approach to manage deer populations in Japan (Kaji et al. 2010). Furthermore, intensive studies on seasonal migration and habitat use, age structure, and reproductive conditions have been started in model study sites (in and around the ANP). The Scientific Council was established by the prefectural government with biologists and statisticians in 1999. It has played an important role as an advisory board for sika deer management. Figure 32.8 shows the framework of consensus building and decision-making for the CMPS (Kaji et al. 2006).

1. Design stage: Assessment of problems and acknowledgement of uncertainty are important when formulating the management plan.
2. Implementation stage: We consider harvest as a manipulation, and it should be implemented in the action plan. The Hokkaido Government, municipalities, and hunters perform harvest activity.
3. Monitoring stage: The HIES monitors and analyzes population trends using spotlight counts, aerial counts, and questionnaire surveys. The hunter association and government officers cooperate in spotlight counting.
4. Evaluation stage: The Scientific Council evaluates the results of monitoring and management outcomes and estimates the population size via harvest-based models.
5. Adjust stage: The Hokkaido Government incorporates the results and new information into future decisions and discloses such information to the public. For example, the Hokkaido Government announced an underestimation of the initial

population size and then improved the management plan (Hokkaido Government 2000).

The Ministry of the Environment, Forestry Agency, and the Hokkaido Government managed the Shiretoko WNHS with Shari and Rausu Towns. The Shiretoko Regional Liaison Committee was formed to ensure coordination between governmental agencies and related organizations, such as the Fishery Association (Sakaguchi 2016). The Shiretoko Nature Foundation mainly conducts monitoring and culling based on annual action plans. A scientific council consisting of wildlife experts was established to review and advise research and monitoring projects (Sakaguchi 2016). This committee also plays an important role in the management of the Shiretoko WNHS.

32.7 Perspectives

We divided the island into three districts, the East, the West, and the South, as management units in the CMPS (Fig. 32.2). However, the management units should be determined based on genetic information. Ou et al. (2014) showed that the three subpopulations were maintained from the 1990s to 2000s based on mitochondrial DNA analysis and suggested that the northwest and southwest had different subpopulations within the West District. Therefore, we should revise the management units for the CMPS.

Because the hunter population is decreasing (Fig. 32.1), an encouragement for the utilization of deer as a natural resource, hunter training, and support are required to maintain hunting systems. A new community-based management trial, combining recreational hunting with experts and hunter education, has been underway in Nishiokoppe and Shimukappu Villages, Hokkaido (Igota and Suzuki 2008). Venison has a high value as game meat, which is called “gibier” in Europe, and it has become popular in recent years among Japanese (Ohtaishi and Honma 1998). The Hokkaido Government prepared “the guideline for utilization of venison” and “the manual of hygiene for venison” in 2006 and recommended the use of harvested deer. For a sustainable resource management in the long term, maintaining hunting systems and recruiting young hunters are important.

When there is a weak density dependence on population growth, natural regulation of sika deer cannot be expected (Ueno et al. 2010; Kaji et al. 2010). Population control is necessary to prevent habitat destruction. In particular, to avoid native impacts on natural ecosystem in national parks and nature reserves, culling systems are important because hunting efficiency would be too low for volunteer hunters in these areas. Our goal to conserve biodiversity is the development of culling systems and training cullers. The Yezo Deer Association started the educational programs of the Deer Culling Certificate (DCC) in 2015 (Yezo Deer Association 2020). Hunting as resource management and culling for ecosystem management would result in a synergy for the adaptive management of sika deer in the future (Kaji et al. 2010).

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Chapter 33
Deer Management in the Tanzawa Mountains, Kanagawa Prefecture

Koji Nagata and Atsushi Tamura

Abstract Kanagawa Prefecture formulated the "Sika Deer Management Plan" in 2003. The plan has a unique feature that was instituted after a decline in natural vegetation and forest ecosystems in high-altitude zone of the Tanzawa Mountains. The plan contains four management goals: conservation and restoration of biological diversity, sustaining stable sika deer population in the Tanzawa Mountains, reduction in agriculture and forestry damage, and prevention of sika deer colonization out of the Tanzawa Mountains. Kanagawa Prefecture fixes the management goal and practitioner per three areas established in the Tanzawa Mountains based on the plan, and various projects are implemented in collaboration with Kanagawa Prefecture and municipalities. Kanagawa Prefecture mainly conducts constructing of deer exclosures and culling in natural vegetation conservation area. Deer densities tend to decrease by conducting various measures; however, numerous management units still remain with high deer densities, and vegetation recovery is partial. Additionally, deer densities have tended to increase around the Tanzawa Mountains. We have obtained outcomes like understory cover incline to some extent, whereas we need to continue deer management to solve the remaining problems.

33.1 Introduction

The Tanzawa Mountains is located within 100 km southwestern of Tokyo and has about 50,000 ha northwestern in Kanagawa Prefecture (Fig. 33.1). Kanagawa Prefecture has a population of 9.2 million, the second largest population behind Tokyo

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K. Nagata (✉)
Division of Nature Conservation, Natural Park and Wildlife, Kanagawa Prefecture Natural Environment Conservation Center, Atsugi, Japan
e-mail: sikaeru@ta2.so-net.ne.jp

A. Tamura
Division of Forest Research and Nature Restoration Planning, Kanagawa Prefecture Natural Environment Conservation Center, Atsugi, Japan
e-mail: tamura.7qh1@pref.kanagawa.jp

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Fig. 33.1 Location map of Kanagawa Prefecture and the Tanzawa Mountains

Metropolitan in Japan. The Tanzawa Mountains has pristine nature irrespective of the suburb of Tokyo, Kawasaki, and Yokohama. The top of the Tanzawa Mountains is Mt. Hirugatake (1673 m in elevation). Natural forests like beech (*Fagus crenata*) dominate over 1000 m of the mountains, and cedar (*Cryptomeria japonica*) and cypress (*Chamaecyparis obtusa*) plantations or secondary forests like oak (*Quercus serrata*) dominate from foot to halfway of the mountains. The piedmont area is used for agriculture. The impact of forest ecosystems by sika deer (*Cervus nippon* Temminck) in the Tanzawa Mountains markedly increased since the 1990s, and Kanagawa Prefecture formulated the “Sika Deer Management Plan” (SDMP) to dissolve strong deer impact in 2003. Based on over 15 years of experiences on the SDMP, we report the history of setting the SDMP, the implementation system, vegetation restoration by deer exclosures and deer culling, and monitoring results.

33.2 Deer Problems in the Tanzawa Mountains

Sika deer had widely inhabited in the Kanto Plains of Sagami and a part of Musashi (present Kanagawa Pref.) till the early eighteenth century; however, sika deer had reduced their distribution and had disappeared from the Kanto Plains for human cultivation and vermin control with rising human population in the early nineteenth century and had been confined only in the Tanzawa Mountains (Taguchi 1997). Analyzing genetic information and the demographic history of recent recovery from a bottleneck suggested that the Tanzawa population is distinct from the Kanto population (Yuasa et al. 2007; Chap. 35).

In Japan, sika deer had dropped their population due to hunting against a backdrop of drastic human population increase and modernization between the late nineteenth century and the early twentieth century (Ministry of the Environment

2015). Kanagawa Prefecture, therefore, had gradually prohibited deer hunting since 1938 and protected deer till 1953 when hunting of male deer was open. Female deer had been excluded from game animals with Wildlife Protection and Hunting Low in 1947. Overt illegal hunting by US army occupation forces was widespread in the Tanzawa Mountains in 1953 because it was in turmoil after the Second World War (Forestry Division of Kanagawa Prefecture 1984), causing the sika deer population to decrease at 50 individuals level in the Tanzawa Mountains after the hunting season in 1954 (Shibata and Murase 1964; Furubayashi et al. 1997). Therefore, Kanagawa Prefecture had prohibited deer hunting all across the prefecture area from 1955 to 1970. The deer protection measures increased in deer population and expanded the distribution of deer. The period (1955–1970) corresponded approximately to the restoration era of denuded forests and expansive afforestation era of cedar and cypress toward the increase in timber production, and it lead to the situation that deer damaged planted cedar and cypress seedlings in the Tanzawa prefectural forests and then private forests in the submontane districts were also damaged. Kanagawa Prefecture has controlled harmful deer since 1967 against forestry damage, constructed exclosures around plantations since 1970, set up four hunting areas in the middle abdomen of the Tanzawa Mountains to open male deer hunting in 1970, and pursued an excellent balance between the development of agriculture and forestry and conservation of deer.

Constructing exclosures and growth of plantation forest decreased the feeding plants for deer, and wildlife protection area was set up in high altitudes of the mountains. Besides, snow accumulation declined in recent years, concentrate and increase their population in natural forests over 1000 m in elevation. The dense population at high altitudes declined the natural vegetation and damaged the forest ecosystem. There was a decline in dwarf bamboo (*Sasamorpha borealis*) around the plantation in the late 1970s and a beech forest in the late 1990s (Furubayashi and Yamane 1997) and changes in species composition of beech forests (Ohno and Ozeki 1997). In the piedmont, agricultural damage by deer has constantly occurred at the same time as natural vegetation decline. In contrast, we felt apprehension for malnutrition of deer.

Through these processes, Kanagawa Prefecture instituted the “Sika Deer Management Plan in Kanagawa Prefecture (hereafter, SDMP)” in 2003 with three targets: (1) conservation and restoration of biological diversity, (2) sustaining stable sika deer population in the Tanzawa Mountains, and (3) reduction in agriculture and forestry damage (Kanagawa Prefecture 2003). To date, 2020, the fourth SDMP (planning period: 2017–2021) is proceeding adding the fourth target on “prevention of sika deer colonization out of the Tanzawa Mountains.”

33.3 Sika Deer Management Plan in Kanagawa Prefecture (SDMP)

33.3.1 Feature of the Plan

Sika deer inhabits all across the Tanzawa Mountains in Kanagawa Prefecture, and the population is expanding their habitat range into the Hakone Mountains, the Kobotoke Mountains, and Oiso Hills (Fig. 33.1). The SDMP, therefore, covers all of the municipal areas west of the Sagami River; however, the management project has continued only in the Tanzawa Mountains since 2003.

Most of the prefectures in Japan instituted the Sika Deer Management Plan following an increase in agriculture and forestry damage (Iijima 2018). By contrast, Kanagawa Prefecture has a unique feature of the plan instituting after a decline in natural vegetation and forest ecosystems in high-altitude zone (approximately over 1000 m in elevation) of the Tanzawa Mountains. Today, sika deer seriously impacts forest ecosystems all around the prefectures (Ministry of the Environment 2015), of which Kanagawa Prefecture has early grappled with conserving forest ecosystems across the country.

Kanagawa Prefecture also instituted both the “Plan for Tanzawa-Oyama Nature Restoration” and the “Five-year Action Plan for Water Source Environment Conservation” since 2007 and is working on conservation and restoration of the Tanzawa Mountains, which corresponds to water resource for a Kanagawa Prefecture resident. Sika deer management project is ranked in both Plans. Various projects are proceeding based on both Plans, and the target toward reducing the effect of sika deer on the forest ecosystem and conserving it accords closely with that of the SDMP; thus, each project organizes and works together possible.

33.3.2 Implementation System

SDMP zones the Tanzawa Mountains into three areas (natural vegetation conservation area, habitat management area, and damage control area) according to land use and sika deer impacts (Fig. 33.2). Kanagawa Prefecture has advanced deer population management, deer habitat management, and damage control measures in collaboration with relevant organizations like municipalities according to the management goal of each area (Table 33.1). Considering the relationship between zoning and practitioner, Kanagawa Prefecture mainly implements the projects in the natural vegetation conservation area and habitat management area, and municipalities mainly implement the projects in the damage control area.

Kanagawa Prefecture established the Natural Environment Conservation Center in 2000. The center conducts prefectural deer culling, construction of deer exclosures, and monitorings to verify the effects of the projects in the high-altitude zone of the Tanzawa Mountains toward recovery of its natural vegetation.

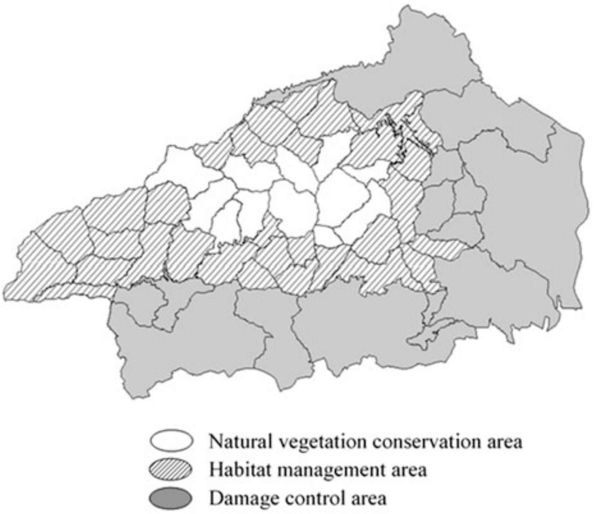


Fig. 33.2 Zoning in the Tanzawa Mountains (Kanagawa Prefecture 2017a). *Small parcels correspond to management units

Table 33.1 Management goal, major endeavors, and implementation system for deer culling in the Sika Deer Management Plan in Kanagawa Prefecture (SDMP)

Area	Main goal	Main projects	Main population control method and practitioner	Conducted area (unit)
Natural vegetation conservation area (high-altitude zone)	Decline in deer density and early recovery of vegetation	Prefectural construction of deer exclosures and prefectural deer culling	Culling for conserving natural vegetation by Kanagawa prefecture	Management unit where natural vegetation decline within wildlife protection area
Habitat management area (middle-altitude zone)	Stable continuation of sika deer population under the condition that understory vegetation does not decline	Cooperation practice of prefectural deer culling and forest management	Culling for building a base of deer habitat by Kanagawa prefecture	Forest management area for water source environment conservation and its margin
Damage control area (low-altitude zone)	Prevention of sika deer colonization around agricultural landscape and reduction in agriculture and forestry damage	Damage control measures and deer culling by municipalities	Culling for reducing agriculture and forestry damage by municipalities	Agriculture and forestry damaged area and its margin

*Derived from Kanagawa Prefecture (2017a)

*In habitat management area, culling is practiced for conserving natural vegetation and for reducing agriculture and forestry damage according to the condition of the area

*In hunting area within each three areas, hunting is practiced

Throughout the country, the Center is a novel organization that implements various projects such as wildlife management, national park management, prefectural forest management, public awareness activity, and research and survey in one organization. The center has an advantage of implementation system which can follow the PDCA cycle for vegetation recovery under the same organization.

Kanagawa Prefecture formulates an implementation plan for the sika deer management project, which integrates prefectural plan and each municipal plan every fiscal year. The implementation plan is formulated through consultation in Kanagawa Comprehensive Measures Conference for Birds and Wildlife, which consists of relevant administrative organs and academics, and is published on the Internet. Besides, the implementation plan uses information such as deer densities and captured heads aggregated in increments of 56 management units (hereafter, unit) zoned in the Tanzawa Mountains.

33.3.3 Budget

Project of natural vegetation recoveries such as deer culling, construction of exclosures, and monitorings by Prefecture is almost wholly dependent on the tax for Water Source Environment Conservation by Kanagawa Prefecture. The tax is the excessive taxation of prefectural residents' tax as a source of revenue to promote special measures ranked as a Five-Year Action Plan for Water Source Environment Conservation. The Action Plan is based on a Policy Outline for Water Source Environment Conservation and Restoration, of which Kanagawa Prefecture states the whole projects for conservation and restoration of water source environment for 20 years since 2007. The significant measures of the Action Plan are accretion cutting in plantation forests, which are lacking management, and soil conservation of natural forests, including the construction of exclosures, which use the tax since 2007. Prefectural deer culling was not ranked as the Action Plan till 2011, and the culling had been conducted without using the tax for Water Source Environment Conservation till that time; however, it has been ranked since 2012 because the effects of accretion cutting in plantation forests had not been produced sufficiently due to heavy deer grazing, and soil erosion had occurred on those forests. The cost to hire wildlife rangers, i.e., professional cullers, as temporary workers, is an appropriated tax for Water Source Environment Conservation by Kanagawa Prefecture. Sika deer management projects can be enriched using the tax in addition to a former source of revenue.

33.4 Projects to Conserve Natural Vegetation

Each division of Kanagawa Prefecture and Kanagawa Prefecture Natural Environment Conservation Center cooperate on the measures for the targets of the SDMP (Table 33.1). This section reports the measures for conservation and restoration of biological diversity which characterize sika deer management in the Tanzawa Mountains.

33.4.1 Deer Exclosures for Vegetation Conservation

The exclosures function to protect plants from deer grazing and as seed sources to outside the exclosures. The exclosures have been constructed as natural park projects since 1997 before the formulation of the SDMP and thereafter have been also constructed to relate to the SDMP and other plans like the Five-year Action Plan for Water Source Environment Conservation. Since 1997 the exclosures have been constructed at natural forests in special protection area and class 1 special area in Tanzawa-Oyama Quasi-National Park, which are high-altitude zone approximately over 1200 m in elevation. We constructed several small- to medium-sized wire-mesh exclosures, the size of which ranges from 30 × 30 m to 50 × 50 m, 1.8 m high, on one location to disperse risks of exclosures broken by natural disturbance (Fig. 33.3). Exclosures are frequently broken by fallen trees, heavy winds, and fallen snows every year and are checked and repaired accordingly.

There are 732 exclosures with 91.6 km in length and 81.6 ha in the area at the end of March 2020 (Kanagawa Prefecture Natural Environment Conservation Center unpublished data). There seems to be no area where many exclosures like the Tanzawa Mountains have been constructed in natural forests. Based on the effects of vegetation recovery of natural forests by exclosures (Tamura et al. 2005; Tamura 2020), exclosure systems have been expanded on secondary forests of low-altitude zone (Fig. 33.4) or cedar and cypress plantations aiming to sift to mixed forests with broad-leaved trees involve in various forest types though the area of constructed exclosures is limited compared to that of natural vegetation.

33.4.2 Prefectural Culling

Deer population control based on the SDMP is divided into culling by prefectural or municipal and sports hunting. Prefectural or municipal culling is practiced with a clear aim, conducted area, and practitioner according to the management goal of each area (Table 33.1).

Kanagawa Prefecture practices culling aiming to conserve natural vegetation and build a base of deer habitat management. “Prefectural culling aiming to build a base

Fig. 33.3 Condition of several years after the construction of a deer exclosure in beech forest

of deer habitat management" is the culling practiced around plantations for sifting to mixed forests in middle-altitude zone. Forest management is not always practiced as a project of the SDMP, but it leads to the improvement of deer habitat by an increase in understory vegetation. By contrast, the concentration of deer into managed forest prevents understory vegetation from growing, and it is necessary for culling to cooperate with forest management to balance between understory vegetation and deer habitat.

Prefectural culling is practiced by the Kanagawa Prefecture Natural Environment Conservation Center, and the Center makes deer culling plan to decrease deer density and keep its low density based on the monitoring results, past culling results, and information about forest management in each unit every fiscal year. Based on the deer culling plan in each unit, the Center practices prefectural culling, which is done by the Kanagawa Hunting Club and the wildlife rangers, with commission of the Kanagawa Prefecture Natural Environment Conservation Center. Prefectural culling is mostly practiced in wildlife protection area.

Fig. 33.4 A deer exclosure in secondary forest

33.4.3 Kanagawa Hunting Club

Kanagawa Hunting Club is a party comprised of hunters residing in Kanagawa Prefecture, and it was established for the purpose of improvement in hunting ethics, hunting optimization, and game animal protection. The members of the club have controlled harmful birds and mammals at the request of local municipalities before the formulation of the SDMP, and prefectural culling by the club is different from the control kill.

The Kanagawa Hunting Club has conducted deer culling using drive hunting with dogs under the SDMP by Kanagawa Prefecture. Controlling deer population by drive hunting has a merit in that hunters can apply their experience in hunting; however, it has difficulties in inaccessible locations because it needs to allocate shooters within a certain range in a short time and uproot deer with hound dogs.

The Kanagawa Prefecture Natural Environment Conservation Center appoints culling dates and locations, and the Kanagawa Hunting Club selects practitioners of culling out of the club members on each date. Practitioners preliminarily attend a seminar of prefectural deer culling, and cull deer, measure the body size of culled deer, and obtain a sample of body for analysis on the day. Each work is conducted under the appointment of the head of practitioners, who coordinates each record and submits a final report to the Kanagawa Prefecture Natural Environment Conservation Center.

Prefectural culling by the Kanagawa Hunting Club shows large variations in culling proficiency because practitioners are replaced by other members every culling day. Some practitioners may meet other practitioners first on the day, indicating communication problems and lack of cooperation among practitioners. Nevertheless, disciplined works are conducted under the head of practitioners.

33.4.4 Wildlife Rangers

Wildlife rangers conducted deer culling in mountain ridge that is difficult to access. They possess professional knowledge about sika deer, hunting license, and hunting gun permit, and they are staffs sent from a temp agency to the Kanagawa Prefecture Natural Environment Conservation Center based on Worker Dispatch Law.

Wildlife rangers conducted deer culling by stalking or cruising culling through a detailed action plan based on the deer culling plan in each unit (Katase et al. 2020). They have mobility which they can take culling locations and methods suited to the occasion according to changeable weather peculiar to mountainous region and the mountaineers, and it is a characteristic point for culling by them. However, we have no system, which public agency staff themselves cull deer through the year, across the country, and therefore we practice prefectural deer culling by them through a trial-and-error process including procedures about related laws and regulations, such as duty management, security management, and technical acquisition of culling.

33.4.5 Monitoring

We need monitoring to validate the effects of deer culling and exclosures and revise the measures in the SDMP. In the fourth SDMP, the testable management goal by monitoring is set according to areas (Table 33.2), and comprehensive evaluation is conducted based on various monitoring results. The indicators in Table 33.2 are

Table 33.2 Implement target in each area at the point of the Fourth Sika Deer Management Plan in Kanagawa Prefecture (SDMP)

Area	Indicator for target achievement	Result (2011–2015)	Result (2016–2020)
Natural vegetation conservation area	Point number which understory vegetation cover is more than 50%	14 points out of 25 points	21 points out of 25 points
Habitat management area	Point number which understory vegetation cover is more than 25%	10 points out of 27 points	15 points out of 27 points

*Derived from Kanagawa Prefecture (2017a)

*The point in the table indicates the vegetation survey plots set up in management area analyzed from vegetation survey, which are conducted inside and outside an exclosure plot per unit at regular intervals. To grasp the condition of the deer population, we conduct a deer population survey by block count method, distribution survey by pellet group count method, analysis of a sample of culled body, and collecting information about hunting. Also, we coordinate culled deer location by both wildlife rangers and the Kanagawa Hunting Club using GIS and use it to consider dates and locations of the following year culling effectively. We conduct a deer population survey per unit and comprehend deer density distribution and its change. Besides, we survey deer density in areas culled by wildlife rangers and the Kanagawa Hunting Club every year and use the result to validate the effects of prefectural culling. Multiple indices obtained from the above survey results are used to evaluate the SDMP.

33.5 Status of SDMP Implementation

33.5.1 Culling Result

Figures 33.5 and 33.6 show the change in the annual capture number of deer since 2003 when the SDMP began. The capture number drastically increased during the second SDMP (2007–2011); this depends on easing hunting regulations (whole opening of female deer) and enhancing prefectural culling (increasing in area and frequency). The capture number by prefectural culling was below 100 during the first SDMP, but it increased by ca. 200–400 during the second SDMP. Furthermore, it increased to ca. 400–600 since 2012, because both prefectural culling around

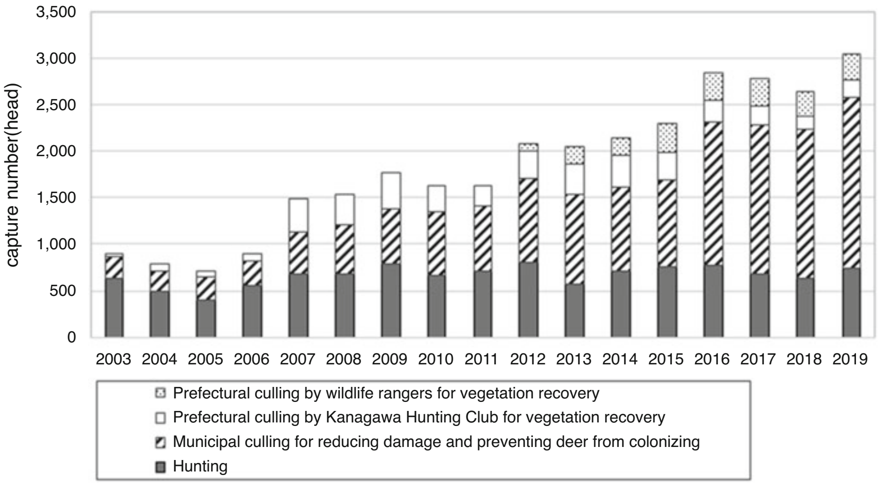


Fig. 33.5 Change in capture number of deer (all target area of the Sika Deer Management Plan in Kanagawa Prefecture)

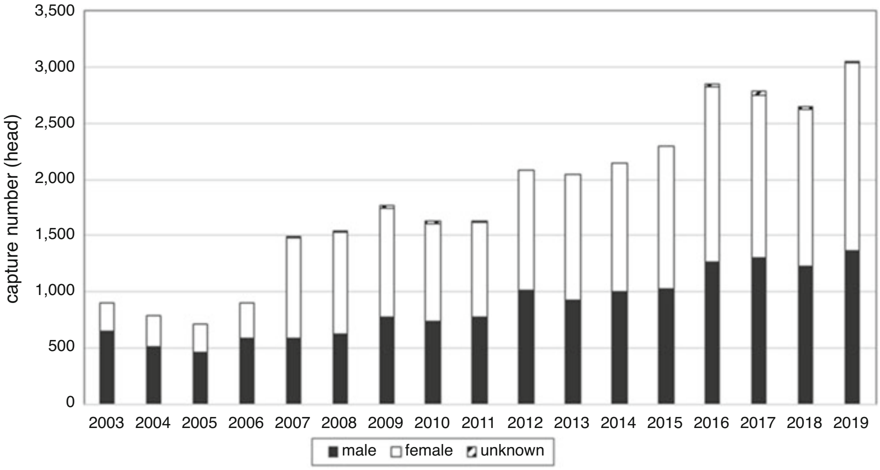


Fig. 33.6 Change in capture number of deer. Black bars indicate the number of males, and white bars indicate that of females

artificial forests by the Kanagawa Hunting Club and prefectural culling around mountain ridges by wildlife rangers have begun using tax for Water Source Environment Conservation by Kanagawa Prefecture.

The capture number by municipal culling drastically increased in 2016, but it may depend mainly on the effect of active culling by introducing capture incentive dispensation (Kanagawa Prefecture 2017b). On hunting, the capture number has fluctuated between ca. 600 and 700 since 2007 when hunting regulations were drastically eased.

33.5.2 Change in Deer Density and Condition of Vegetation Recovery

The deer density tended to decrease in units where prefectural culling has been practiced since 2003 (Fig. 33.7). There were many areas with high deer density over 20 deer/km^2 in the block count method at the beginning of the SDMP, but such areas with high deer density drastically decreased as of 2019. However, there are few units under 5 deer/km^2, and even units where deer density decreased, and some units remain with high deer density over 10 deer/km^2, and there are many areas where the deer density does not tend to decrease in units where prefectural culling has been practiced since 2012 (Fig. 33.8).

Understory vegetation cover increased in the units where deer density decreased, and plants grew quite noticeably in high-light conditions such as open land (Fig. 33.9); however, understory vegetation cover stayed unchanged or decreased in the units where deer density did not decrease (Table 33.3, Fig. 33.10). The

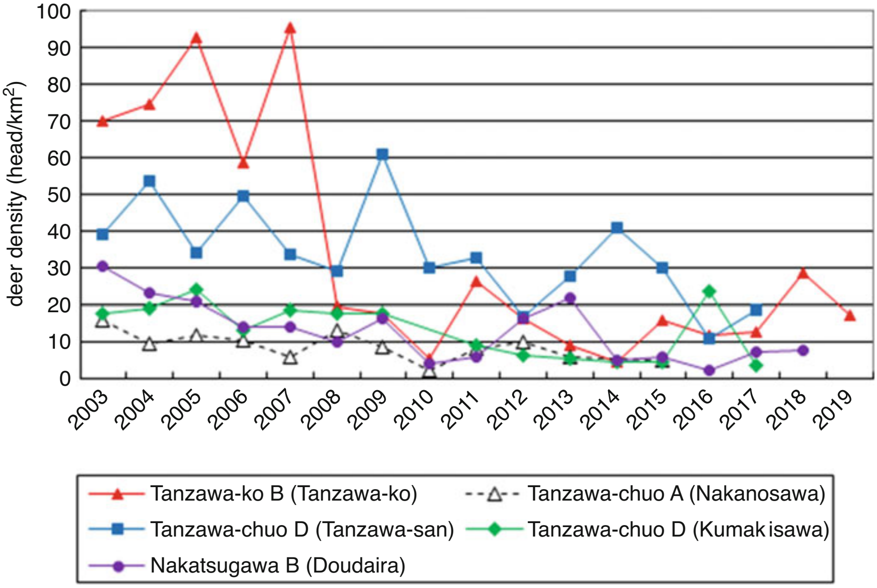


Fig. 33.7 Change in deer densities in units where prefectural culling has been continuously practiced since 2003. *A word in parentheses is an area name where the block counting method is surveyed

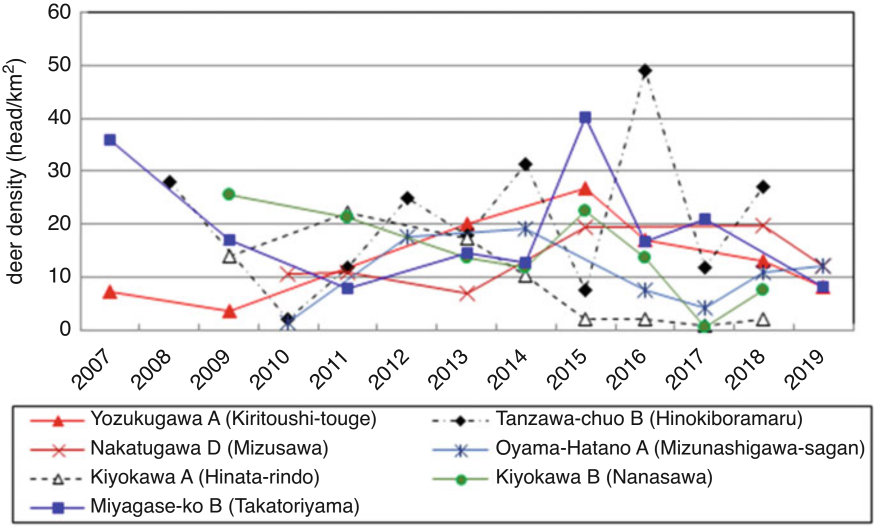


Fig. 33.8 Change in deer densities in units where prefectural culling has been continuously practiced since 2012. *A word in parentheses is an area name where the block counting method is surveyed

Fig. 33.9 Change in vegetation in an open land of management unit where deer density decreased by prefectural deer culling since 2007 (Left; 2003, Center; 2008, Right; 2019)

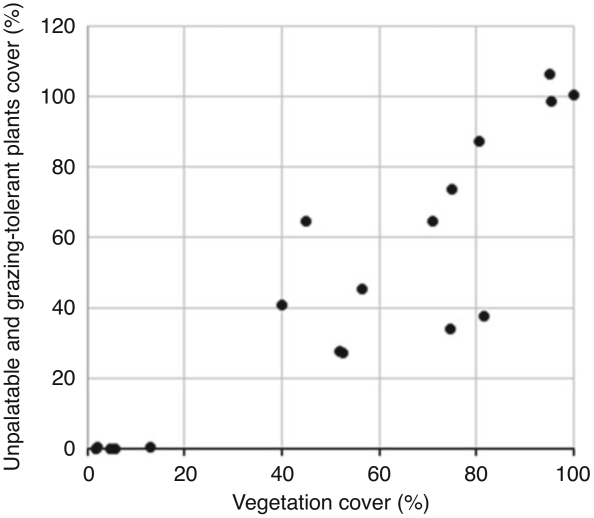
Table 33.3 Variation in vegetation cover at the point of the first and the third Sika Deer Management Plan in Kanagawa Prefecture (SDMP)

Area	Increase more than 10%	Decrease more than 10%	Remain unchanged
Natural vegetation conservation area	5	3	5
Habitat management area	2	0	3

Number of vegetation survey plots
*Variation in vegetation survey plots where deer culling has been practiced since before 2011

Fig. 33.10 Secondary forest where understory vegetation cover does not increase

Fig. 33.11 Relation between understory vegetation cover and unpalatable and grazing-tolerant plants cover (at the moment of the third Sika Deer Management Plan). *The result derived from units where prefectural culling has been practiced since before 2011. **Unpalatable and grazing-tolerant plant covers are greater than vegetation cover in some units because they are separately measured



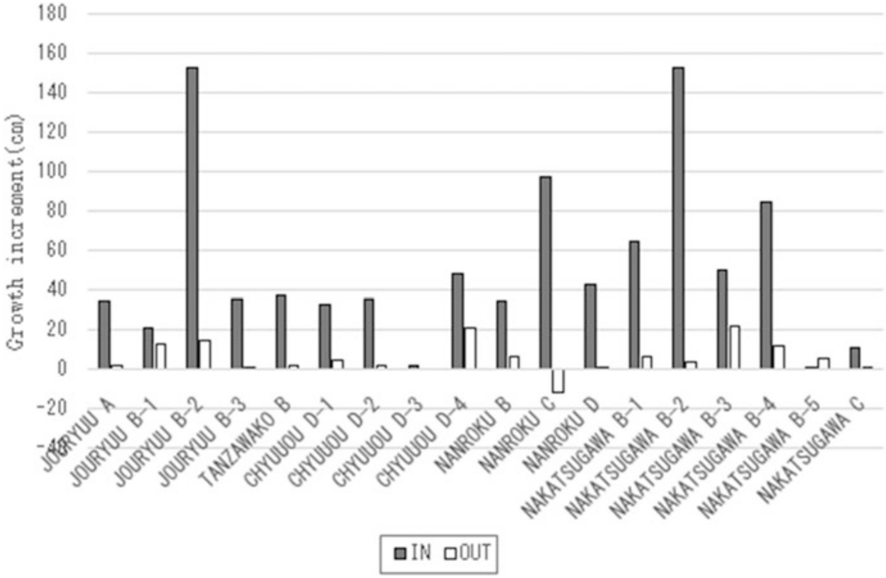


Fig. 33.12 Tree seedlings' growth increments inside and outside deer exclosures. *The result was calculated from the average height of tree seedlings at the first SDMP and the third SDMP in units where prefectural culling has been practiced since before 2011

vegetation cover of unpalatable or grazing-tolerant herbs dominates in the area the cover increased (Fig. 33.11), and regenerated tree seedlings do not grow noticeably (Figs. 33.12 and 33.13).

Fig. 33.13 Natural forest where understory vegetation cover is increased, but most of it is unpalatable herbs for deer

In contrast, plants such as tree seedlings and herbs grow dramatically inside the exclosures (Fig. 33.12 and 33.14). However, the process for vegetation recovery differs by vegetation types and its decline conditions at the timing of constructing exclosures, and vegetation does not always recover toward pre-decline conditions (Tamura 2010). Additionally, deer density is zero inside the exclosures, and the process for vegetation recovery inside the exclosures can differ from that of the outside of the exclosures where deer inhabits in low density. Tamura (2016) reports that the similarity entirely differs between the composition of soil seed bank outside a deer exclosure and that of vegetation inside the exclosure. He indicated that it was difficult for overgrazed forests by deer to recover their original species composition even after sika deer density decreased (Tamura 2016; Chap. 26). Tanentzap et al. (2012) also suggest several reasons for the delay in vegetation recovery after deer population reduction. Therefore, vegetation recovery may not always follow the same process by reduction of deer density.

A conservation and restoration of biological diversity, which is one of the targets of the SDMP, set growth of regenerated tree seedlings and development of storied structure as the goal; however, vegetation recovery can be uncertain, and achieving the goal may need prolonged periods. Therefore, to evaluate the short-term effect of the projects, we require flexibility about goals toward not only the condition inside

Fig. 33.14 A deer exclosure in which trees and shrubs have grown inside

the exclosures but also the recovery of ecosystem function according to monitoring results.

33.5.3 Population Status Surrounding the Tanzawa Mountains

Deer sightings have tended to increase around the Tanzawa Mountains during the past decade, and some areas in the Hakone Mountains have the same density of pellet group as those of the Tanzawa Mountains (Fig. 33.15). Also, damage to crop production comes into existence, and the capture number of municipal culling tended to increase (Kanagawa Prefecture 2020). The impact of sika deer to the forest ecosystem is partial in the Hakone and the Kobotoke Mountains at this time; however, it can be aggravated if deer density continued to increase. Prefectural culling is practiced on the ridgeline of forest zone in the Hakone Mountains, where municipal culling is not practiced. The forest floor is covered with dense bamboo and others, and is vistaless. Therefore, in the Hakone Mountains, it is difficult to use the same culling methods as the Tanzawa Mountains. Furthermore, the construction of exclosures is still a very small portion of the Mountains.

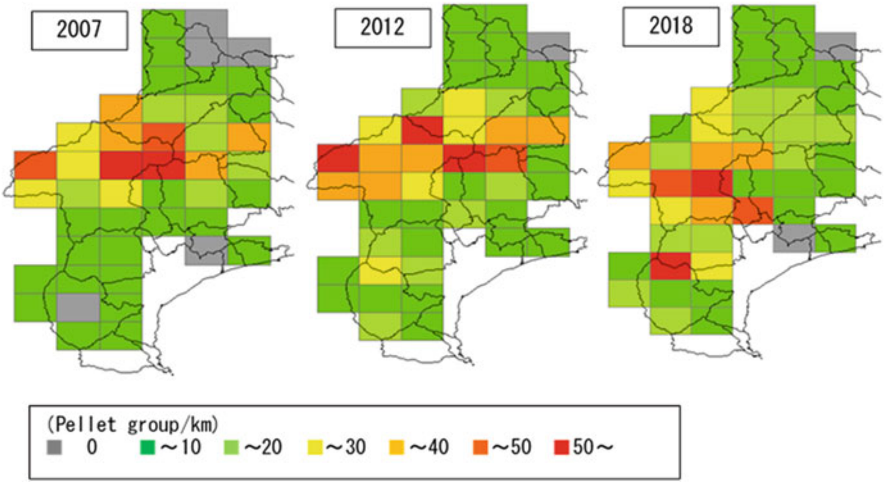


Fig. 33.15 Results derived from surveys of the pellet group count method

The effect of sika deer on natural vegetation was rare in the country in the 1990s when the decline in natural vegetation by deer has been revealed in the Tanzawa Mountains. We had insufficient knowledge of the effect of deer on natural vegetation at that time; therefore, various measures were not taken till vegetation decline by deer densification had grown into a serious problem. We have experienced that we require a substantial effort to recover retrogressed vegetation, and we need to advance practical efforts in collaboration with relevant organizations based on precautionary principles in the Hakone Mountains and others.

33.6 Toward the Next Decade

We have achievements such as a decline in deer densities by the measures of the SDMP, and we must continue the measures to achieve goals; however, we also have many problems with the current measures in terms of continuousness.

Exclosures are steady for vegetation recovery but cannot be constructed all over the undulating mountains and can be limited by constructing on moderate slopes only like a ridgeline. Additionally, we must consider the cost for maintaining exclosures (including the removal in the future) and impacts on other large mammals. Therefore, vegetation recovery by exclosures is local, and deer population control is needed to continue.

Further, the current implementation system of prefectural culling by the Kanagawa Hunting Club has several problems. The club, with a commission of the Kanagawa Prefecture Natural Environment Conservation Center, is not a company, and the practitioners are not professional for culling. The practitioners participate in prefectural culling through their holidays, and it means a limitation of culling frequencies. They also cull with acquired hunting techniques for personal hobbies, and there is significant variability among their techniques. Besides, the continuousness of culling by the Kanagawa Hunting Club is also a significant problem because the members of the club are increasingly aging.

Wildlife rangers are professional for culling. On the other hand, there are no education institutions and systematical training programs for professional cullers. Therefore, the fact is that wildlife rangers have mastered techniques with practicing culling as an extension of their hobbies, just like the Kanagawa Hunting Club. Also, culling by wildlife rangers is an experimental endeavor using Worker Dispatch Law, and the implementation system is quite insecure because Kanagawa Prefecture has no fabric to staff culling practitioners continuously within its administrative organization.

We also have problems with "sustainability of sika deer population." Originally, sika deer had evolved adaptively in the habitat of plains, the management which keep deer stably in mountains contains fundamental difficulties. Besides, deer behavior and its habitat would be influenced if environmental change such as felling forest has frequently occurred; however, the relation is nearly unknown. It is still the case that we stay in cooperation for conforming deer culling area to forest felling area. We need further endeavors such as planning forest management and deer culling in an integrated manner with grasping inhabiting deer situations.

Kanagawa Prefecture has ever conducted constructing exclosures and deer culling on severe retrogressed vegetation area of the Tanzawa Mountains, leading to partial outcomes like understory cover incline. However, deer impact has expanded on other areas such as the Hakone and the Kobotoke Mountains during that time. Kanagawa Prefecture has responded to that problem by the existing deer culling system, and it can be diffuse measures. It is urgent that a new system be introduced for deer management on a large area including the Hakone Mountains and others.

We must continuously implement the projects of the SDMP to solve the above problems. But tax for Water Source Environment Conservation by Kanagawa Prefecture will be finished being collected in the 2026 fiscal year. Also, tax revenue and talent will decrease in the future depopulating society. In such circumstances, we must discuss whether deer management is needed to continue for Kanagawa Prefecture residents, and if so, we must immediately discuss how we practice deer management in declining budgets and talents.

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Chapter 34
Adaptive Management of Sika Deer in Hyogo Prefecture

Shun Takagi, Daisuke Fujiki, and Mayumi Yokoyama

Abstract The Hyogo Prefecture Government implemented a sika deer management plan in 2000 and has monitored and analyzed various data relevant to deer population status and damage to agriculture and forest ecosystem. Population status has been monitored by fecal pellet-group count survey, hunting reports, and body condition parameters. Agricultural damage has been monitored by a questionnaire survey for agricultural settlements. Ecological damage has been monitored by understory vegetation and was evaluated as the shrub-layer decline rank (SDR). Deer population monotonically increased from 2002 to 2010 when intensive population control was implemented in Hyogo Prefecture. After the control, population density and agricultural damage have decreased in municipalities which have a high achievement rate of harvest quota. The serious declines of shrub-layer vegetation were observed mainly at the center of Honshu region of Hyogo Prefecture, where deer density was relatively high. Though the speed of forest degradation may become moderate with the progress of the population control practice, the decline of shrub-layer may still exceed the recovery of vegetation. To prevent or reduce these adverse effects, short-term and long-term target densities were set in the deer management plan and were consistent with the annual harvest target based on population dynamics. In the future, a practical management strategy should be proposed for each municipality based on fine-scale monitoring and analyses.

34.1 Population Status of Deer in Hyogo Prefecture

Hyogo Prefecture (135 E 35 N) is located in the center of Honshu Island, Japan. Deer distribute at two regions, Honshu Island and Awaji Island, and deer distribute across prefectural borders in Honshu region. In the 1970s, the distribution area in Hyogo was restricted at the central area in Honshu region and southern area in Awaji Island.

S. Takagi (✉) · D. Fujiki · M. Yokoyama
Institute of Natural and Environmental Sciences, University of Hyogo, Wildlife Reserarch Center, Hyogo, Tamba, Japan
e-mail: takagi@wmi-hyogo.jp; fujiki@wmi-hyogo.jp; yokoyama@wmi-hyogo.jp

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Since the late twentieth century, their distribution area has expanded nearly twice within four decades (Inoue and Takagi 2019). As the population is growing, damages to agriculture and forestry become serious. To reduce these damages, the Hyogo Prefecture Government implemented a sika deer management plan in 2000 (Hyogo Prefecture 2000). Ahead of other prefectures in Japan, the government has allowed hunters to hunt female deer since 1994 and has extended the hunting period for deer and the quota of female deer to more than one per day since 2003. Within a framework of adaptive management, population and damage control should be planned, conducted, and improved based on the scientific evidence supported by the analysis of monitoring data. To establish a management target to reduce deer population size and damages, Wildlife Research Center, Hyogo, has monitored and analyzed various data relevant to deer population status, damage to agriculture, and forest ecosystem (Fujiki and Takagi 2019; Sakata et al. 2009). In this chapter, we reviewed the current status and achievement of sika deer management in Hyogo Prefecture.

34.2 Monitoring System of Deer in Hyogo Prefecture

34.2.1 Monitoring of Deer Population

Indices of sika deer density have been annually monitored by fecal pellet-group count survey and hunting reports since 2000 when the first management plan was established. Line-transect census of pellet-group counts were conducted at about 100 of 5 km transects located at mountain ridge during late October to early November, before hunting season (Hamasaki et al. 2007; Sakata et al. 2009). The number of observed fecal pellet-groups per 1 km route was treated as an index of deer density. All hunters submitted hunting reports after hunting season. For the gun hunting, hunters recorded the date and 5 km grid code hunted and the number of deer (as well as wild boar) that they observed and harvested in each grid and on each day. For trap hunting, hunters recorded the date and grid code and the number of trap established by trap types, including box trap, snare trap, and fence trap. The number of deer that they harvested in each 5 km grid and on each day was recorded by trap types. Sightings per unit effort (SPUE) by gun hunting and catch per unit effort (CPUE) by box and snare trap hunting were annually calculated based on hunting records and were used as density indices (Fig. 34.1a). The number of deer harvested during hunting season in each grid was calculated by hunting reports. The government also collected the number of deer harvested by nuisance control conducted by the municipalities.

To evaluate the population condition of sika deer in Hyogo Prefecture, we have been monitoring the biological attributes, such as fertility, body fat, food habits, and body size since 2002 (Yokoyama 2009). We try to clarify these condition parameters in response to the environment and population density. With the increase in population size, venison consumption as a local food resource has increased, and

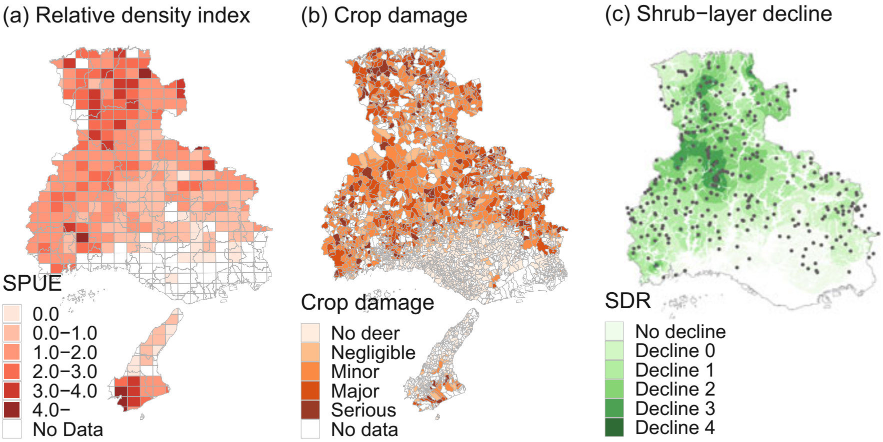


Fig. 34.1 The basic monitoring data representing deer population status and its agricultural and ecological impacts in Hyogo Prefecture. (**a**) SPUE as an index of population density, (**b**) crop damage score in agricultural settlements, and (**c**) shrub-layer decline rank (SDR) in 2018. SDR was scored by a six-point scale; no decline and decline 0 (mild decline) to decline 4 (serious decline)

monitoring for hepatitis E virus, parasites, and chronic wasting disease (CWD) is also being conducted regularly to assess disease risk (Yokoyama 2012).

34.2.2 Monitoring of Agricultural Damage and Ecological Impact

Agricultural damage has been investigated by a questionnaire survey for agricultural settlements since 2004 (Kuriyama et al. 2018). The representative of settlement scores the crop damage on a four-point scale (negligible, minor, major, serious) by each animal species annually (Fig. 34.1b). The mean reply rate for agricultural settlements was more than 80%.

Ecological damage to the forest ecosystem has been monitored by understory vegetation since 2006 (Fig. 34.1c). Although the impact of understory vegetation had been reported at a local scale at that time (Osaki 2006; Fujiki et al. 2006), it remains unclear the spatial spread of deer effects on forest ecosystems. The shrub-layer decline rank (SDR) has come to be a simple but accurate measure of deer-related declines in the shrub-layer vegetation of deciduous hardwood forests (Fujiki et al. 2010). The SDR can be determined by a labor-saving method based on a visual categorization of shrub-layer vegetation cover together with signs of deer browsing, as it has a strong linear relationship with the observation frequency of deer (Fujiki 2012a; Kishimoto et al. 2010). Due to its easy application, SDR contour maps have been created and updated in Hyogo Prefecture and some neighboring prefectures (Fujiki et al. 2014; Koda et al. 2014; Tsunoda et al. 2017; Fukumoto et al. 2018).

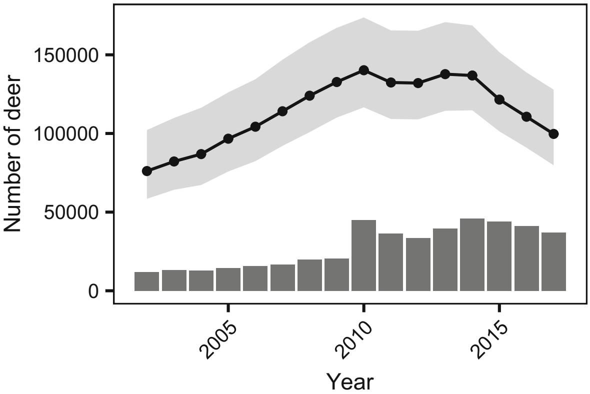
34.3 Population Management Practices Based on the Monitoring Data

34.3.1 Estimation of Population Dynamics and the Effect of Population Control

Sika deer population dynamics were estimated using a state-space model that integrated population dynamics, harvest process, and observations (Harvest-based Estimation: Iijima et al. 2013; Fukasawa et al. 2020; Chap. 4). To estimate regional trends in population dynamics, we built a database for municipal-level monitoring data that included the number of culled and hunted deer, fecal pellet density, sightings per unit effort (SPUE), and catches per unit effort (CPUE). At the prefectural level, population dynamics responded to the population management practice, with a change in trend from increasing to decreasing numbers (Fig. 34.2; Takagi 2019). The estimated number of individuals monotonically increased from 2002 to 2010 when intensive population control was implemented in Hyogo Prefecture. After the intensive population control, more than 30,000 deer have been harvested annually. The proportion of females in the harvest data before and after intensive population control was 50–54% and 57–62%, respectively. Since then, the population has gradually decreased because harvest intensity may have exceeded annual population growth. In 2017, there remains about 100,000 deer (95% CI: 79,777–127,820), which is about two thirds of the peak value in 2010.

At the municipal level, an increase in population density occurred in most cities prior to intensive population control in 2010. Since then, various population trends have been observed: decreases, leveling-off, and continual increases (Fig. 34.3). Because population expansion and the introduction of intensive control varied between regions, dissimilarities in population trends may have occurred.

Fig. 34.2 Deer population dynamics in Hyogo Prefecture. Posterior distribution of estimated population size (line, median; gray fill, 95% credible intervals) and harvest level (gray bar) were shown



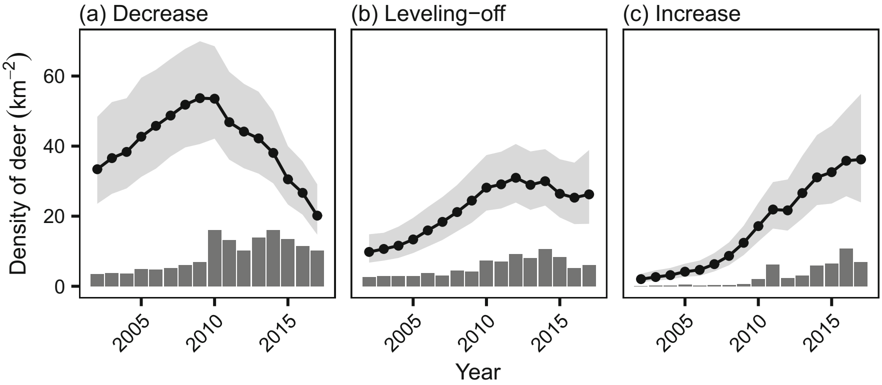


Fig. 34.3 Various deer population dynamics at municipal level in Hyogo Prefecture. (**a**) Decreasing after the intensive population control, (**b**) leveling-off, and (**c**) monotonically increasing. Posterior distribution of estimated population density (line, median; gray fill, 95% credible intervals) and harvest level (gray bar) were shown

34.3.2 Evaluation of Population Condition

Sika deer populations in Hyogo Prefecture are of medium body size, with adult male body mass at 60 kg and adult females 40 kg on average (Yokoyama 2009). During the 1980s, when the population was increasing, the pregnancy rate of female deer was high at over 80% for both yearlings and adults (Osaki et al. 2001; Yokoyama et al. 2003; Koizumi et al. 2009). However, the pregnancy rate of yearlings declined to 12.5% in 2011–2015 (Matsukane and Yokoyama 2018), and the average population density at the prefectural level reached about 30 deer/km^2 in 2010, indicating that density-dependent effects continued to be observed in the pregnancy rate of yearlings.

Body fat accumulation was low throughout the year, with males showing an increase in accumulated fat in August before the rutting season but little change in body fat accumulation during the rest of the season (Yokoyama 2009).

Characteristics of food habits were able to utilize the leaves of evergreen broad-leaved trees during the winter season (Yokoyama 2009), which is also considered a characteristic of sika deer in western Japan and a factor in maintaining high densities even when the understory vegetation declines.

As for diseases, we have been analyzing the status of viruses, parasites, and CWD following an outbreak of hepatitis E virus in 2003; in a nationwide survey in 2004, Hyogo Prefecture analyzed samples of more than 300 animals and confirmed that the antibody prevalence was 3.1% in 2004 (Matsuura et al. 2007). Since then, few antigens have been identified (Morimitsu 2019), and the possession of hepatitis E virus in sika deer has been determined to be low. In terms of parasites, liver fluke (*Fasciola* spp.) and *Dicrocoelium dendriticum* have been identified in 10–20% of cases, and CWD has provided specimens for analysis at the National Institute of Animal Health, National Agriculture and Food Research Organization for periodic evaluation (Yokoyama et al. 2012). However, there has been no positive information to date. The Hyogo Prefectural Government has issued the guidelines for using sika deer for venison based on disease information.

34.3.3 Agricultural Damage and the Factors Affecting Them

As a result of the questionnaire survey, the score of crop damage in agricultural settlements correlated to deer density indices, including SPUE and CPUE (Kishimoto 2010). In addition, damage by deer was well explained in a landscape context; severe impacts of deer were observed at agricultural settlements with a high percentage of forest cover within a 1000 m buffer (Fig. 34.4; Takagi et al. 2018). These results suggested that it is essential to account for both the surrounding forest area and deer density for effective implementation, planning, and evaluation of the management of agricultural damage. For example, in settlements with a moderate percentage of forest (Fig. 34.4b), intensive population controls will be effective because there was a significant relationship between damage level and deer density index. By contrast, in settlements with a high percentage of forest (Fig. 34.4c), population control and damage control, such as the introduction of a protective fence, will be needed because the damage level was relatively high irrespective of deer density. Note that CPUE is roughly correlated to estimated density of deer in the area (Takagi 2019); this index may reflect intensity of occurrence to boundary of forest and agricultural field where box traps were usually set.

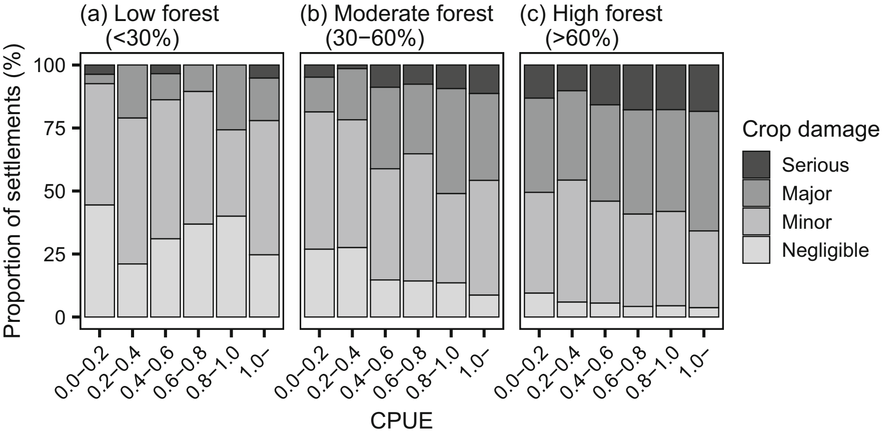


Fig. 34.4 The relationships between agricultural damage by sika deer, forest area surrounding agricultural fields, and box trap CPUE as density index. (**a**) Settlements with low percentage of forest (0–30%), (**b**) moderate percentage of forest (30–60%), and (**c**) high percentage of forest (60%–)

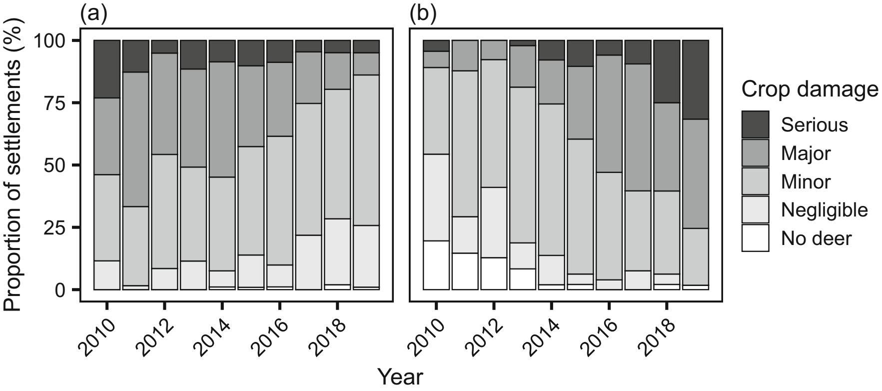


Fig. 34.5 The contrasting trends in agricultural damage assessed by questionnaire survey in two municipalities. (**a**) Damages become less serious in municipality with high achievement rate of harvest quota. (**b**) Damages become more serious in municipality with low achievement rate of harvest quota

The intensive population control in Hyogo Prefecture has achieved certain results for reducing agricultural damage by deer. In 2010, when the density was thought to be the highest, deer cause severe damage to agriculture and forestry, 220 and 250 million yen per year, respectively. Since then, intensive population control has reduced population density as well as damage levels. In 2017, the damage to agriculture and forestry decreased to less than half of the peak, 110 and 70 million yen per year, respectively. Similar to the population trend mentioned above, not all municipalities decrease damage by deer. A numerical target of harvest intensity was set for each municipality depending on deer density and forest area. Agricultural damages showed significant declines in municipalities which have a high achievement rate of harvest quota. On the other hand, damages become more serious in low achievement rates (Fig. 34.5).

The effectiveness of damage controls such as the introduction of protective fence was evaluated (Yamabata et al. 2018). At the prefectural level, the proportion of agricultural settlements that reported major or serious damage exhibited about a plateau from 2011 to 2016. A total of 250 settlements, introduced a protective fence, displayed a decline in the proportion of major or serious damage (from 67% in 2011 to 47% in 2016). In particular, those that made extensive efforts to introduce fences displayed a marked decrease (from 65% in 2011 to 32% in 2016).

34.3.4 Effects on Understory Vegetation and Forest Ecosystems

Monitoring of SDR clarified the effects of deer browsing on forest vegetation at the prefectural level. The serious declines of shrub-layer vegetation were observed in

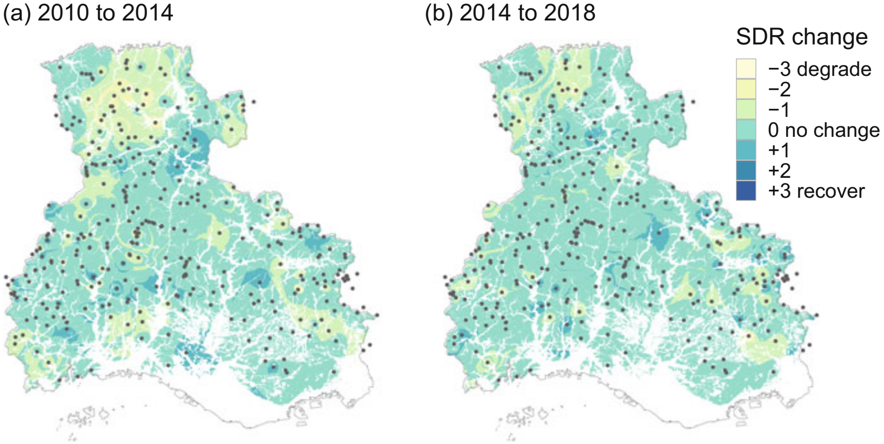


Fig. 34.6 The differences in shrub-layer decline rank (SDR) (**a**) between 2010 and 2014 and (**b**) between 2014 and 2018. Scores represent the degree of degradation (−3 to −1) or recovery (+1 to +3) of SDR in 4 years

2006, mainly at the center of Honshu region of Hyogo Prefecture, where deer density was relatively high (Fujiki et al. 2010). As a result of quadrennial monitoring, about 40% deciduous forests had degraded in 2010 in contrast with that in 2006 (Fujiki 2012b, 2017). Since then, about 20% forests had degraded from 2010 to 2014, and about 10% forests had degraded from 2014 to 2018 (Fig. 34.6). Though the speed of forest degradation may become moderate with the progress of the population control practice, the decline of shrub-layer may still exceed the recovery of vegetation.

Deer browsing indirectly affects forest ecosystem via declines of shrub-layer vegetation. Soil erosion frequently occurred at the stand where half of the understory vegetation was disappeared by deer browsing, and the area with erosion had expanded with the decline of shrub-layer vegetation (Uchida et al. 2012). Spillover effects on animals were also reported; SDR degradation negatively correlated with the appearance of shrub-dwelling birds, including Japanese bush warbler *Horornis diphone* (Seki et al. 2014), and the decline of a number of butterfly species (Kondo 2017).

The understory vegetation will be affected by deer browsing at a long time scale. Since the amount of future vegetation is determined by browsing pressure and growth of vegetation, the current status of vegetation should be a major determinant of future vegetation. A cumulative logistic regression model revealed that 5-year averaged SPUE was well correlated to SDR in 2006 when the first SDR survey was conducted (Kishimoto et al. 2010). After that, to analyze the effect of present vegetation status on future vegetation, we updated a cumulative logistic regression model, which include SDR in a past survey as well as 5-year averaged SPUE as explanatory variables. Results showed some insights into the future vegetation response. First, if mean SPUE level at the prefectural scale decreased to 1.0 in 5 years, the model predicted that the once degraded forest would never recover the

SDR in 5 years. Second, if the SPUE level decreased to 0.5 in 10 years, some recoveries of SDR are expected. Furthermore, if the SPUE level decreased to 0.5 and keeps its level for a long time, the SDR will recover in the broad area of the prefecture. Note that SPUE, a deer density index, can't be monitored in the area where gun hunting was not permitted, and the number of gun hunters will decrease in the future. Relationship between trends in deer density and response of SDR should be confirmed.

34.3.5 Setting a Goal of Deer Population Management Based on the Monitoring Data

Monitoring and estimating deer population dynamics can predict the future of deer population under certain management scenario. In 2010, when the deer population had increased, population estimation and prediction were conducted for the first time (Sakata et al. 2012). As a result, the annual harvest level at that time (20,000 deer/year) will not suppress population increasing. To reduce the population level in the future, more than 30,000 deer have to be harvested. Following this prediction, the Hyogo Prefecture Government has set the numerical target for deer harvest at 30,000 deer/year. Since then, more than 30,000 deer have been caught annually (Fig. 34.7). The numerical target for population management has been reviewed based on the updated evidence, supported by the analysis of monitoring data.

As a result of analyses for the relationships between deer density index and damages to agriculture and forest, the target density for reducing these adverse effects could be established. In the deer management plan developed in 2017, 5-year and 10-year goals were set (Hyogo Prefecture 2017). The short-term goal was set to prevent an increase in agricultural damage and prevent degradation of forest understory vegetation compared with the levels at 2017. The long-term goal was to reduce agricultural damage by half and recover the forest understory vegetation at about 20% of the deciduous forests. These targets will be achieved with

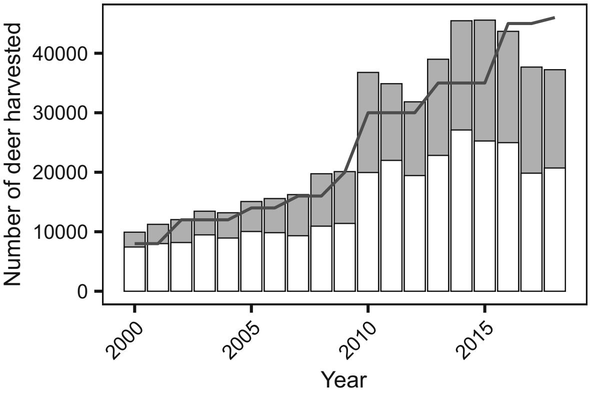


Fig. 34.7 The number of deer harvested in Hyogo Prefecture. Hunting (white) and nuisance control (gray) were shown. Solid line represents annual target for deer harvest

SPUE level decreased to 1.0 and 0.5 in 2021 and 2026, respectively. These targets based on damage level were consistent with the annual harvest target based on population dynamics.

34.4 Future Directions

In recent years, adaptive deer management in Hyogo Prefecture has been achieving some successes, including reduction of population density and decreases of agricultural damage. These results heavily depend on continuous monitoring of the population, analyzing data, and revising the management strategy. In contrast with many other prefectures, Hyogo Prefecture established the institution specializing in wildlife management, Wildlife Research Center, Hyogo, where expert staff and researchers contribute to planning, coaching the management technique, and analyzing scientific data. This may be a good example for the prefecture where the deer population remains to increase. Finally, we discussed ongoing problems, which are expected to be solved by an adaptive management framework.

As a result of population management, overall density decreases at the prefectural level but increases in some municipalities. In addition, deer density determined the intensity of damage by deer. Accounting for these spatial heterogeneities in deer density and landscape structures in a broad scape, it is difficult to solve problems using uniform management goals and management strategies like an intensive population control previously implemented in 2010. A practical management strategy should be proposed for each municipality based on fine-scale monitoring and analyses (Iijima et al. 2013). In recent, we try to visualize population density and the number of harvests at a fine scale such as settlement level. Collecting fine-scale data for density, capture, and crop damage will support an on-site decision-making.

Population management in a range-expanding area is challenging. In 2012, deer capture was recorded at the Western Rokko Mountains, where apart more than 20 km from the edge of the distribution range of deer. The Rokko Mountains is an important habitat for endangered plant species and has a high priority for biodiversity conservation in Hyogo Prefecture. As an initial response to deer occurrence, we have examined deer distribution in this area and established a system for culling deer. As results of camera trapping and survey of damage to palatable plants, deer were suggested to distribute mainly in the national government park. A test culling was conducted in the park from 2014 to 2018, and fecal pellet density was significantly reduced during a period of test culling. These findings suggest that culling efforts are necessary even when the capture efficiency drops due to low population density (Yokoyama and Numata 2019). To adopt the future spread of deer distribution, it is needed to establish the monitoring methods applicable for the initial stage of range expansion, including identifying the route and direction of expansion and an effective capture method in a low deer density area.

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Chapter 35
Subpopulation Structure Based on Landscape Genetics as a Management Unit

Takashi Saitoh and Chisato Terada

Abstract Deer management programs establish management units (MUs) to reach the goal. MUs are frequently shaped in the social rather than the biological context, and thus the inconsistency between biological- and social-based MUs could occur. We reviewed researches identifying genetic clusters in sika deer populations of Japan and analyzed the correspondence of MUs in management programs to the genetic population structure in five populations (Hokkaido, Toyama, Tanzawa, Boso, and Yakushima). MU-related problems were found in every management program. We genetically and demographically analyzed the Yakushima population inhabiting a World Natural Heritage Site. Although the management program for the Yakushima population established ten MUs to attain the control- and conservation-oriented aims, we proposed four biological MUs, which were genetically and demographically independent. Further, we discussed how to align the MUs in the Yakushima population.

35.1 Introduction

Caughley (1977) listed the following three problems that wildlife managers should work on to reach the management goal:

(1) Conservation: treatment of small or declining population to raise its density
(2) Sustained yield harvesting: exploitation of a population to take from it a sustained yield
(3) Control: treatment of a population that is too dense, or which has an unacceptably high rate of increase, to stabilize or to reduce its density

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T. Saitoh (✉)
Field Science Center, Hokkaido University (Retired), Sapporo, Japan
e-mail: takashisaitoh@frontier.hokudai.ac.jp

C. Terada
Wakayama Experimental Forest, Field Science Center, Hokkaido University, Wakayama, Japan
e-mail: cterada@fsc.hokudai.ac.jp

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The common thread of these problems is the regulation of population size and growth rate (Shea and the NCEAS working group 1998). Since a management unit (MU) is established to attain the management goal (Strickland et al. 1994), a different MU is postulated for each aim. The first problem should be treated in the largest unit called as the evolutionary significant unit (Ryder 1986), while the latter two should be treated in the smaller unit (MU) more focusing on ecological features. MU, which this chapter focuses on, is crucial for monitoring the abundance and distribution of wildlife (Palsbøll et al. 2007), the prevalence of wildlife diseases including zoonoses (Miller et al. 2020), and the damage from wildlife to agricultural products and ecosystem (Côté et al. 2004). We cannot develop a management strategy without knowing where a population begins and ends (Funk et al. 2012).

MUs are biologically defined as populations of conspecific individuals, among which the degree of connectivity is sufficiently low so that each population should be monitored and managed separately (Taylor and Dizon 1999), and MUs should be large enough to estimate population parameters with desired precision (Strickland et al. 1994; Rosenberry and Diefenbach 2019). However, MUs are frequently shaped in the social rather than the biological context. This is because management programs have considered human-related matters (e.g., administrative district, social requirements, and others), and MU should be easily recognized by hunters (Strickland et al. 1994).

Genetic approaches are often used to delineate MUs, and the recent advances in landscape genetics have greatly enhanced our ability to define population structure. Genetic information helps us identify demographically independent units among which movements are limited. Those biological units are not always concordant with the social-based MUs (Apollonio et al. 2010). The inconsistency between biological- and social-based MUs affects the efficiency of management works because movements across MUs may reduce the success rate of management (Ijima et al. 2015). MU-related problems are listed as four of nine causes of management failure in ungulate populations of Europe (Apollonio et al. 2010). Therefore, MU alignment should be examined from biological and social viewpoints.

In this chapter, we reviewed researches identifying genetic clusters in sika deer populations of Japan and compared MUs established by the deer management program to those genetic clusters. As mentioned above, the inconsistency between biological- and social-based MUs may cause management failure. We discussed how to align the MUs using an example of the Yakushima population inhabiting a World Natural Heritage Site.

35.2 Population Structure and Management Unit

Although not few studies analyze the genetic features of Japanese sika deer populations, the limited number of studies provided information about population structure in association with MU. This section focused on four populations (Hokkaido, Toyama, Tanzawa, and Boso) for which both biological and management information about MU is available. The Yakushima population, another population with the two pieces of information, is separately discussed in the next section, focusing on MU alignment.

35.2.1 Hokkaido Population

Hokkaido is the northernmost island of Japan (Fig. 35.1). It is the second-largest (77,984 km^2) but less populated island compared to other central islands of Japan. The sika deer was abundant throughout Hokkaido Island before the colonization by Japanese in the late nineteenth century. Overexploitation, habitat loss, and heavy snowfall caused a rapid decline in deer abundance around 1900. Following deer protection policies, a grassland increase, the wolf extinction, and a decrease in hunters' number, the sika deer population recovered (Kaji et al. 2010).

Ou et al. (2014) compared the spatial genetic structure of the Hokkaido population between two periods (1991–1996 and 2008–2010), using both microsatellite and mtDNA markers. The two microsatellite-based subpopulations were consistently observed in the northern and southern regions for decades. In contrast, mtDNA-based structure became simple from four (the first period) to three subpopulations (the second period). Two northern subpopulations fused into one probably because of deer movement from high- to low-density subpopulation. The microsatellite-based structure that reflects the effect of gene flow by both males

Fig. 35.1 The locations of five sika deer populations on which this study focused. The Kanagawa and Chiba Prefectural Governments manage the Tanzawa and Boso populations, respectively. The Yakushima population is managed by the Kagoshima Prefectural Government. Dotted lines indicate prefectural borders

and females suggests the potential for future local adaptation. Therefore, the authors recommend the use of the microsatellite-based structure from an evolutionary perspective. In contrast, the mtDNA-based structure is recommended for female-targeted management because the mtDNA-based structure indicates maternally structured groups.

The main goal of the Conservation and Management Plan for Sika Deer (CMPS) for the Hokkaido population is to reduce the deer damage to agriculture and forestry products and other human-deer conflicts through culling and hunting deer (Hokkaido Prefecture 2017; Chap. 32). Since other social requirements are relatively minor, CMPS can simply establish MUs considering the demographic independence of subpopulations. However, CMPS targeted the eastern part of the population in the beginning, because the deer damage mainly occurred in the eastern region, and then defined MUs as western and eastern subpopulations. Subsequently, the scientific board of CMPS added the MU system based on the northern and southern subpopulations, considering the suggestion of Ou et al. (2014). CMPS has strongly promoted female culling and hunting for the effective control of the deer population, and the mtDNA-based structure should be considered as MUs.

35.2.2 Toyama Population

Toyama is a prefecture located in the central region of Honshu Island, facing the Japan Sea on the north side (Fig. 35.1), and has a population of 1,044,588 (June 2019). The 30% of the prefecture's area is designated as national parks. The sika deer in Toyama were thought to have become extinct in the first half of the twentieth century, immigrated in the early 2000s from neighboring prefectures, and expanded. Eva and Yamazaki (2019) suggested two genetic clusters using 11 microsatellite loci, but a high admixture was detected. Together with mtDNA analyses (Yamazaki 2018), they suggest that the Toyama population is derived from immigrants from the east and south.

The Toyama Prefectural Government listed three aims of the deer management in the 2017 version of the program (Toyama Prefecture 2017): (1) reduction of agricultural and forestry damage, (2) prevention of deer expansion, and (3) prevention of intrusion into national parks. However, the program does not establish MUs corresponding to its aims and could not include the information about the population structure from subsequent genetic studies (Yamazaki 2018; Eva and Yamazaki 2019).

35.2.3 Tanzawa Population

Kanagawa is a prefecture located in the central region of Honshu Island, bordering Tokyo to the north (Fig. 35.1), and has the second most population of Japan at

9,216,009 (September 2020). Konishi et al. (2017) analyzed the spatial genetic structure of the population (162 individuals) in Kanagawa and surrounding areas (Kanto) using 10 microsatellite loci. They revealed two genetic clusters, which occurred in the Tanzawa mountain range and the Kanto mountain areas, respectively. Analyses using the D-loop of mtDNA support the genetic identity of the Tanzawa population (Yuasa et al. 2007; Hata et al. 2019), and its demographic history (a recent recovery from a bottleneck) is suggested to differ from that of the Kanto population. The local government develops a conservation strategy corresponding to this population structure.

The Kanagawa Prefectural Government, covering the Tanzawa mountain range, aims mainly to keep the Tanzawa population at an adequate density and prevent its expansion to neighboring areas in the 2017 version of the management program (Kanagawa Prefecture 2017). They set 56 MUs, ranging from 3.3 to 82.6 km^2, and carry out the culling and excluding of deer. However, partly because of the small unit sizes, the correlation between the intensities of unit-specific culls and the reduction of deer density was very weak (Takeshita et al. 2017), and the management effects are insufficient to achieve the goals (Chap. 33). Therefore, those MUs should be revised considering deer movement among the current MUs. A detailed analysis of population structure may help to infer deer movement among the units (see a case study on the Yakushima population in this chapter).

35.2.4 Boso Population

Chiba Prefecture mostly consists of the Boso Peninsula of Honshu Island, which encloses the eastern side of Tokyo Bay (Fig. 35.1), and has the sixth most population of Japan at 6,278,060 (June 2019). The sika deer in Boso are thought to have had a continuous distribution range in the past, but the population may have become small and isolated because of urbanization and high hunting pressure in the first half of the twentieth century. Following deer protection policies, the Chiba population recovered, and agricultural damage has been reported since 1978.

Yoshio et al. (2009) revealed two genetically distinctive clusters using nine microsatellite loci. The microsatellite-based structure is consistent with the results from mtDNA analyses (Yoshio et al. 2008), and the population was separated into the eastern and western subpopulations. They considered that the Boso population consisted of genetically different lineages, which had been spatially separated, and they came into contact in the vicinity of a local road along a steep-walled ravine.

The Chiba Prefectural Government established three zones for deer management in the 2017 version of the program (Chiba Prefecture 2017): (1) a conservation-oriented zone, (2) a control-oriented zone against agricultural and forestry damage, and (3) a prevention zone against deer expansion. The target deer density is set 3–7/km^2, ≤ 3/km^2, and none/km^2 for the three zones, respectively. Although the program describes its aims and zoning, the correspondence relationship between the zoning and MUs is unclear. Since the subpopulation boundary crosses the control-oriented zone, an independent demographic approach for the eastern and western subpopulations within that zone is required.

35.2.5 Goals of Japanese Deer Managements

Uno et al. (2007) reviewed 29 deer management programs established by prefectural governments and classified their management goals into (1) to avoid local extinction, (2) to reduce deer-human conflicts, (3) to reduce deer population sizes, and (4) to conserve ecosystems. Since the third aim (the population size reduction) is a practical aspect of the second (the deer-human conflict reduction), the management goals can be reorganized into (a) the conservation, (b) the deer-human conflict reduction, and (c) the ecosystem management. Sustained yield harvesting listed by Caughley (1977) has not been adopted as a management goal in Japanese management programs. It is a specific feature of Japanese deer managements.

The concept of MU has not penetrated well into Japanese deer managements. The guideline for deer management programs provided by the Ministry of the Environment does not define the MU system explicitly (Ministry of the Environment 2021a), and Uno et al. (2007), the most comprehensive review of Japanese deer managements, did not include the MU system into evaluation elements to assess the management programs.

Many programs establish management zones based on social requests without considering the biological structure of deer populations. Control- and conservation-oriented zones are usually established for agricultural and natural reserve areas, respectively. However, the management effects may be diluted when deer move between these zones. It is hard to achieve a management goal without establishing MUs that are demographically independent. The inconsistency between zoning and biological MUs would surface in other management programs with the accumulation of genetic and demographic studies of deer populations. Therefore, MU alignment would be one of the keys to developing a management strategy. We discuss how to align the MUs in the next section, using an example of the Yakushima population.

35.3 MU Alignment: A Case of the Yakushima Population

Yakushima is an island ca. 60 km off the southernmost major island (Kyushu Island) of Japan (Fig. 35.1). The island, 504.88 km^2 in area, has a population of 12,040 (December 2020). The about one-fifth of the island (107.47 km^2) has been designated as a World Natural Heritage Site since 1993 owing to the unique remnant of an ancient forest. Further, 209.89 km^2 of the island, which includes the World Natural Heritage areas, is managed by the Ministry of the Environment as the Yakushima National Park. The island is visited by 300,000 tourists every year.

The Yakushima population is recognized to have increased from the late 1980s (Tsujino et al. 2004; Koda et al. 2008) and has impacted on agricultural crops (Kagoshima Prefecture 2017) and the natural vegetation (Tsujino and Yumoto 2004, 2008; Koda et al. 2008). The Kagoshima Prefectural Government established the Specified Wildlife Conservation and Management Plan (SWCMP) for controlling sika deer in 2012 and revised it in 2017 (Kagoshima Prefecture 2017).

SWCMP aims at keeping the deer density at an adequate level, under which ecological interactions are in balance for the World Natural Heritage Site, and at reducing the deer population to moderate the deer-human conflict (e.g., the deer impact on the crops and the natural vegetation). The 2017 version of SWCMP established 10 MUs assuming the river system may limit the deer dispersal.

35.3.1 Landscape Genetics and Management Units

Terada et al. (2021) analyzed the spatial genetic structure of the Yakushima population using 12 microsatellite loci. Two and four subpopulations were revealed by STRUCTURE (stN and stS) and GENELAND (glN, glE, glS, and glW) software. All pairwise genetic differentiations (F_{ST}) between the two and four subpopulations were significant. The location of the western boundary between stN and stS corresponded with the Nagata River, which is one of the major rivers of Yakushima running between MU-8 and MU-9 (Fig. 35.2), whereas any landscape or biological feature could not be identified for the eastern boundary. Further, except for the Nagata River, rivers did not contribute to shaping the STRUCTURE-based structure.

Each conservative genetic structure (stN or stS) included several MUs; stN included MU-1, MU-9, and MU-10, while stS did MU-4, MU-5, MU-6, and MU-8 (Fig. 35.2). MU-2 was divided into two parts belonging to stN or stS. In the GENELAND-based structure, glW fitted MU-8. However, other correspondence relationships were not simple. glN included MU-9 and the western part of MU-10; glE included MU-1, the eastern part of MU-10, and the northern part of MU-2; and glS included MU-4, MU-5, MU-6, and the southern part of MU-2.

The GENELAND-based structure did not show the clear congruence with the river system as well as the STRUCTURE-based structure. Although large rivers are suggested to prevent deer to disperse (Coulon et al. 2006; Long et al. 2010; Robinson et al. 2012), Miller et al. (2020) claimed that small- or medium-sized rivers facilitated deer movement. Therefore, the simple assumption that the river system may limit the deer dispersal could not be accepted in the viewpoint from the spatial genetic structure of deer populations.

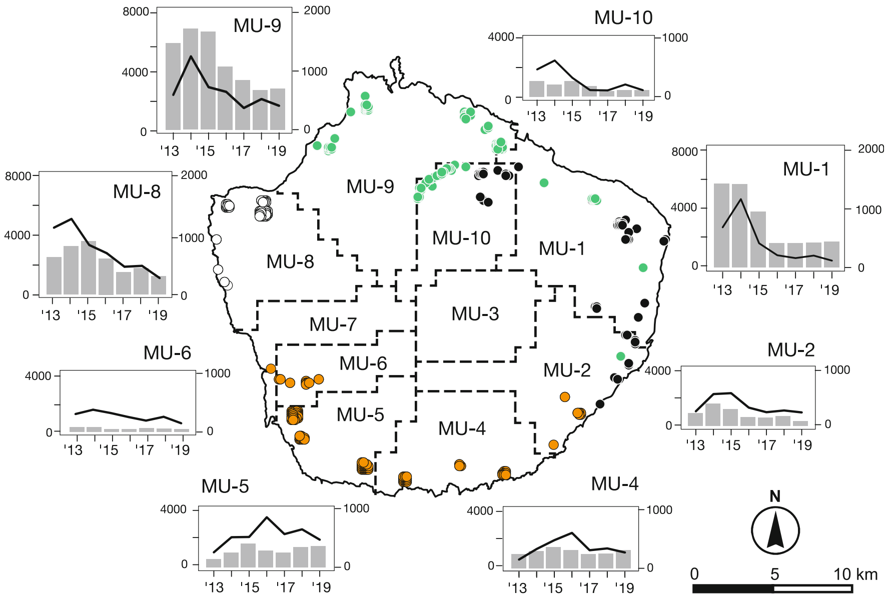

Fig. 35.2 A map of management units (MU1 to MU10) and individual locations of deer samples (circles) for the Yakushima population. The management units (MUs) were established by the Kagoshima Prefectural Government (the Specified Wildlife Conservation and Management Plan (SWCMP) for controlling sika deer, 2017), and broken lines delineate unit boundaries. Terada et al. (2021) revealed two and four subpopulations using STRUCTURE (stN and stS) and GENELAND (glN, glE, glS, and glW) software, respectively. Symbols represent the different subpopulations (glN, glE, glS, or glW). Black circles fringed with white (glE) and green circles fringed with white (glN) belong to stN. White circles fringed with black (glW) and orange circles fringed with black (glS) belong to stS. Estimated deer abundance (line) (Kagoshima Prefecture 2021; K. Shioya, unpublished data) and the number of culled deer (bar) (Ministry of the Environment 2021b) are also illustrated for each MU. The values of the line and bar are scaled on the left axis and right axis, respectively. Years for these panels represent the Japanese fiscal years (April–March). The data are omitted for MU-3 and MU-7 because of no genetic information

35.3.2 Population Trends

MU must be demographically independent (Strickland et al. 1994; Rosenberry and Diefenbach 2019). Kagoshima Prefecture estimated the deer abundance between 2013 and 2019 for each MU (Kagoshima Prefecture 2021; K. Shioya, unpublished data, Fig. 35.2). MU-1, MU-8, and MU-9 held higher abundance in 2013–2014 compared to other units. Subsequently, the deer abundance of MU-8 steadily decreased, while the significant reduction was observed between 2014 and 2017 in MU-1 and MU-9 (Pearson's correlation $r_p = 0.896$, $P = 0.006$). The trends in abundance and culling of MU-4 and MU-5 resembled each other ($r_p = 0.858$, $P = 0.014$). MU-10 exhibited a similar trend in abundance to MU-1 ($r_p = 0.972$, $P = 0.0002$). MU-2 did not show any significant correlation with neighbor units

($r_p = 0.627$, $P = 0.132$ between MU-1 and MU-2; $r_p = 0.382$, $P = 0.397$ between MU-2 and MU-4). The abundance and culling of MU-6 fluctuated at a low level.

MU-8 was independent of neighbors in both population trends and genetic features (glW). MU-1 and MU-9 showed a similar trend in abundance. However, the reduction rate from 2014 to 2019 (1—Abundance2019/Abundance2014) was much higher for MU-1 (0.92) than for MU-9 (0.66), although they suffered similar intensive culling pressure and belonged to the same genetic cluster (stN). In contrast, MU-4 and MU-5, belonging to the same genetic cluster (stS and glS), exhibited a similar trend in abundance under the similar culling condition. Therefore, there was no evidence showing their independence in both population trends and genetic features. The population trend of MU-2, which consisted of individuals from the two genetic clusters (stN and stS), showed a combined pattern of MU-1 and MU-4. MU-10, which consisted of individuals from the two genetic clusters (glN and glE), exhibited the similar declining trend to MU-1 and MU-9, and its reduction rate (0.81) intermediated between those of MU-1 and MU-9. The independence of MU-6 was unclear owing to the data deficiency.

35.3.3 Movements Among MUs

To assess the demographic independence of MUs, we estimated movement ratios among MUs using the software of BayseAss 3.0 (Wilson and Rannala 2003; Fig. 35.3) using the microsatellite data from 280 samples collected by Terada et al. (2021). In this analysis, MU-2 was divided into the northern and southern parts following the results of the STRUCTURE analysis. The northern part was coupled with MU-1 (MU-1’), and the southern part was coupled with MU-4 (MU-4’).

Movement ratios indicate the proportion of immigrants in Fig. 35.3. For example, 0.12 of MU-10 were immigrants from MU-1’, and MU-10 also received immigrants from MU-9 at the same rate (0.12). The proportion of native individuals of MU-10 was 0.68 given in the parentheses, and the remaining proportion (0.08) was the sum of minor movements from other MUs, which are not illustrated. Therefore, the proportion of native individuals could represent demographic independence.

The proportion of native individuals was high in MU-5 (0.91) and MU-9 (0.86). They were also major providers of immigrants to other MUs. MU-9 provided immigrants to MU-1’, MU-6, MU-8, and MU-10, in which immigrants from MU-9 occupied more than 0.1. MU-9 kept relatively high abundance after the reduction in 2015, whereas MU-1’, MU-8, and MU-10 decreased to low abundance (Fig. 35.2). These differences in population trends may explain the deer movements from MU-9 to the decreasing MUs. More samples are needed to discuss the relationship between MU-6 and MU-9 ($n = 9$ for MU-6).

MU-5 provided immigrants to MU-4’ and MU-8, in which immigrants from MU-5 occupied more than 0.1. Particularly 0.21 of MU-4’ consisted of immigrants from MU-5. This was consistent with their similarity in population trends and genetic features (Fig. 35.2); genetic distance between MU-4’ and MU-5 was very

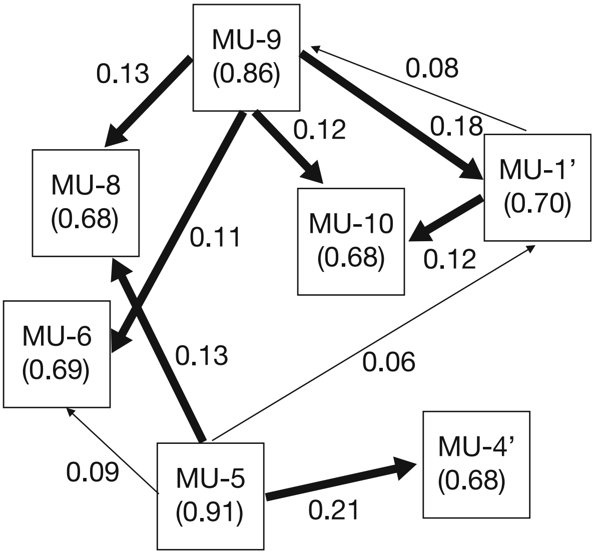

Fig. 35.3 Movement ratios among seven management units (MUs) estimated using BayseAss 3.0 (Wilson and Rannala 2003). Movement ratios indicate the proportion of immigrants in an MU. Arrows indicate the direction of movements. Bold lines show higher movement ratios over 0.1, while movement ratios between 0.05 and 0.1 are illustrated by thin lines. Proportions of native individuals are given in the parentheses. Movement ratios lower than 0.05 were discarded. Sample sizes are as follows: $n = 44$ for MU-1', $n = 29$ for MU-4', $n = 60$ for MU-5, $n = 9$ for MU-6, $n = 41$ for MU-8, $n = 79$ for MU-9, and $n = 18$ for MU-10

close to zero ($F_{ST} = -0.001$). The effect of MU-5 on MU-8 may be indirect because MU-6 and MU-7 are laid between MU-5 and MU-8.

The relationship between the proportion of native individuals and the demographic independence was not simple. The proportion of native individuals of MU-8 was 0.68 and received a considerable proportion of immigrants from MU-9. However, the population trend of MU-8 did not follow that of MU-9 (Fig. 35.2), and genetic distance between MU-8 and MU-9 was significantly higher than zero ($F_{ST} = 0.024$, $P < 0.0001$). In contrast, MU-4', of which the proportion of native individuals was the same as that of MU-8, appeared to depend on MU-5 demographically and genetically.

35.3.4 Biological MUs

The seven MUs could be grouped into four based on the population trends: (1) MU-1 showed a distinct decline from a peak in 2014; (2) the population trend of MU-9 resembled that of MU-1, but its reduction rate (0.66) was lower than the latter (0.92); (3) MU-4 and MU-5 were neighboring units with the similar fluctuating pattern in abundance; (4) MU-8 showed the different population trend from neighbors. In addition to these four trends, MU-2 showed a combined pattern of MU-1 and MU-4. MU-10 exhibited the similar declining trend to MU-1 and MU-9, and its reduction rate (0.81) intermediated between those of MU-1 and MU-9.

This grouping was consistent with the GENELAND-based subpopulation structure. MU-1 and MU-10 were the main components of glE, and both MU-4 and MU-5 belonged to glS. MU-8 and MU-9 corresponded to glW and glN, respectively. Following the genetic clustering, it is recommended to divide MU-2 into the northern and southern parts and couple the northern and southern parts with MU-1 and MU-4, respectively. Similarly, it is favorable to couple the eastern and western parts of MU-10 with MU-1 and MU-9, respectively. Because the GENELAND-based subpopulations were congruent with demographic independence, we commend that SWCMP reconsiders the MU system based on the GENELAND-based subpopulations.

35.3.5 MU Alignment

According to the two main aims of SWCMP, Yakushima can be divided into two zones: the conservation-oriented zone corresponding to the World Natural Heritage Site and the control-oriented zone for other areas. The World Natural Heritage Site roughly consists of MU-3, MU-4, MU-7, and MU-8. The target density differs between the conservation-oriented and control-oriented zones.

There is a serious inconsistency between the above zoning and the biological MUs. MU-4 is included in the World Natural Heritage Site, whereas MU-5 is recognized as the control-oriented zone, although they belong to the same biological MU. Since SWCMP aims to reduce the Yakushima population on the entire island as of 2020, including the conservation-oriented zone, no serious inconsistency has been found between MU-4 and MU-5. However, when the population density decreases to satisfy the request of the conservation-oriented management, a MU-related problem would be elicited. The control-oriented management may request further reduction of the population for MU-5, while the conservation-oriented management may need to mitigate the culling for MU-4. It is insoluble for the management in principle to satisfy these contradictive social requests simultaneously in the same biological MU. Even if we continued an aggressive culling in MU-5, such effort would be diluted by the immigration from the conservation-oriented area (MU-4), in which the culling was mitigated, as Fujimaki et al. (2016) suggested. Therefore, wildlife managers should revise the management goal based on the biological MU in this case.

35.4 Closing Remarks

It is noteworthy that independent units were detected both genetically and demographically in a small island population like Yakushima. Sika deer may behave on a smaller spatial scale than we previously recognized. Although the river system may partly explain the population structure, a deer population could extend crossing a significant river and, on the other hand, could diverge without any conspicuous landscape barrier. Therefore, we have to analyze the population structure of deer without preconception. In this point, a genetic approach is a powerful tool. We can estimate deer movements as well as reveal a cryptic population structure. Genetic connectivity, however, depends primarily on the absolute number of dispersers among populations, whereas demographic connectivity depends on the relative contributions to population growth rates of dispersal vs. local recruitment. Therefore, it is risky to infer the connectivity of subpopulations without the local demographic information (Lowe and Allendorf 2010). The case study of the Yakushima population supports this caveat. Population trends diverged among MU-1, MU-8, and MU-9, although a considerable amount of movement genetically connected them. The genetic information could be more reliable for deer management, together with the demographic information.

The Yakushima population, in which both genetic and demographic information are available, may be an ideal example. The MU system of SWCMP contributed to the reduction of deer abundance which decreased to approximately one-third the abundance from 2014 to 2019, approaching its goal. Population size is variable, and its variability may be enhanced by management treatments. Population structure is also variable (Ou et al. 2014). Therefore, deer populations should be monitored demographically and genetically, and the MU system should be revised following the monitoring results in the manner of adaptive management.

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Chapter 36
Future Challenges for Research and Management of Sika Deer

Koichi Kaji, Hiroyuki Uno, and Hayato Iijima

Abstract A shrinking human population in an area induces changes in land-use patterns; abandoned farmlands across Japan have expanded, which has increased the number and distribution of sika deer populations, resulting in serious damage to agriculture, forestry, and natural vegetation. Deer ranges have expanded close to human settlements, which has increased the risk to human health (deer-vehicle collisions and infectious diseases). Sika deer exhibit high ecological plasticity in movement patterns, density-dependent food switching, and population growth rates depending on habitat quality. Sika deer can survive using low-quality food, and their life history traits such as reproduction rate were rarely affected by their density leading to a sustained high density even in degrading habitats, suggesting that sika deer are highly evolved K-selected species. Under long-term grazing, aboveground body and the seed bank of palatable species will disappear quickly. Thus, the ecosystem resilience will be lost, and the vegetation in the area will not return to its original state even if the deer population is reduced to a lower density by culling. Therefore, the monitoring of forest vegetation and deer population management at low density should be integrated. A wide range of information and evidence-based policymaking should be integrated to successfully manage the highly plastic sika deer populations in a society with a shrinking human population. In the last chapter, we summarized the ecological plasticity of sika deer, focusing on its movement patterns, population dynamics, food habits, and various impacts on ecosystems to deepen our understanding about them. We then considered the role of humans in the ecosystems as users and engineers, which caused drastic changes in deer distribution

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K. Kaji (✉)
Tokyo University of Agriculture and Technology (Retired), Fuchu, Japan
e-mail: kkaji@cc.tuat.ac.jp

H. Uno
Faculty of Agriculture, Tokyo University of Agriculture and Technology, Fuchu, Japan
e-mail: unoh@go.tuat.ac.jp

H. Iijima
Department of Wildlife Biology, Forestry and Forest Products Research Institute, Tsukuba, Japan
e-mail: hayato.iijima@gmail.com

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and population size. The distribution range of deer has expanded to the northern and mountainous areas in response to a decrease in the snow cover period in the past 25 years (Ohashi et al., Ecol Evol 6:7763–7775, 2016). Their distribution range covered 70% of the country as of 2018, and it is expanding at a constant speed, especially in the historical range of the northern part of Honshu (Chap. 2). The expansion of deer distribution is expected to accelerate further with decreasing snow cover period (Chap. 3). In Japan, the human population is shrinking faster than that in the rest of the world. Moreover, the population is concentrated in cities associated with declining primary industries, which has led to a rapid decline in land use and management pressure in rural areas, including a rapid increase in abandoned farmland, a declining hunting population, and an aging population (Tsunoda and Enari, Conserv Biol 34:819–828, 2020). Here, we discuss the future management directions for developing resilient forests and sustainable social-ecological systems in a shrinking society.

36.1 Ecological Plasticity of the Sika Deer

36.1.1 Movement Pattern

Latitudinal Gradient

The Japanese archipelago consists of four large north-south islands: Hokkaido, Honshu, Shikoku, and Kyushu Islands. The migratory behavior of sika deer was more remarkable in northern Japan, including Hokkaido and the northern part of Honshu than in southern Japan, including Shikoku and Kyushu (Table 36.1). This result supports the findings of a previous study (Yabe and Takatsuki 2009; Igota et al. 2009). In eastern Hokkaido, most (77%) deer migrated seasonally, while the remaining population (23%) was sedentary (Igota et al. 2004); 97% of the collared deer in the Oze area, northern Honshu, were migrants (Chap. 11). In central Honshu's Kirigamine area, 65% of the collared deer were migrants, and 35% were non-migrants (Chap. 10). On Kinki and Kyushu Islands, 38% and 10% of the deer were migrants, respectively (Chap. 14). All (100%) collared deer on Shikoku Island were sedentary (Chap. 14). Partial migration is common in large ungulates living in highly seasonal environments, including moose (*Alces alces*, Ball et al. 2001), red deer (*Cervus elaphus*, Mysterud et al. 2011), mule deer (*Odocoileus hemionus*, Nicholson et al. 1997), and roe deer (*Capreolus capreolus*, Cagnacci et al. 2011; Peters et al. 2017). Peters et al. (2017) pointed out that partial migration is a form of behavioral plasticity.

Migration distances were longer in the northern region than in the southern region (Table 36.1). The longest distances (average 54 km) were recorded in eastern Hokkaido (Chap. 8), which is consistent with previous studies (Uno and Kaji 2000; Igota et al. 2004; Hino et al. 2017). In eastern Hokkaido, sika deer have extensive and continuous summer habitats such as pastures and deciduous broad-leaved forests (Kaneko et al. 1998), whereas their wintering range is restricted to a small number of coniferous forests (Sakuragi et al. 2003), resulting in large-scale

Table 36.1 Outline of migration pattern and home range for sika deer from north to south regions in Japan

Regions	Ratio of migrants (%)	Migration distances^a (km)	Home range size (ha)			Site fidelity		Factor of migration	References
			Summer	Winter	All year	Summer	Winter		
Eastern Hokkaido	76.5 (*n* = 51)	58.7 ± 8.9 (F^b, UM^c) 29.0 ± 2.3 (F, DM^d)	125 ± 25 (UM) 123 ± 29 (DM) 66 ± 4(NM^e)	74 ± 19 (UM) 107 ± 17 (DM) 197 ± 36 (NM)	–	High	Low	Snowmelt Forage availability (spring)	Uno and Kaji (2000) Igota et al. (2004)
Western Hokkaido	81.3 (*n* = 16)	10.2–17.7 (F, *n* = 13)	–	–	–	–	–		Tachiki and Yoshida (Chap. 8)
Southern Hokkaido	33.3 (*n* = 15)	7.0–28.0 (*n* = 2)	–	–	–	–	–		
Tohoku (inland)	81.8 (*n* = 11)	11.3 ± 3.3 (*n* = 9)	144 ± 62	223 ± 106	–	High	High	Snowfall (autumn)	Yamauchi et al. (Chap. 9)
Tohoku (coastal)	12.5 (*n* = 8)								
Oze	96.6 (*n* = 30)	25.5 ± 7.6	440 ± 126	360 ± 59	–	High	High	Snow depth	Okumura et al. (Chap. 11)
Okuchichibu	36.8 (*n* = 19)	8.1 ± 4.6	670 ± 170	410 ± 72	–	High	High		
Kirigamine	65.4 (*n* = 26)	9.9 ± 5.7	688 (M^f) 348 ± 380 (F)	– 307 ± 308 (F)	–	High	Low	Snowmelt Temperature	Takii and Izumiyama (Chap. 10)
Southern Japan Alps	90.0 (*n* = 10)	13.0 ± 5.8	106 ± 76(M) 133(F)	145 ± 10 (M) 80(F)	–				
Tanzawa	32.5 (*n* = 40)	8.4 ± 4.7(M) 4.7 ± 1.7(F)	164.3 ± 143.1 (M) 36.9 ± 14.7 (F)	66.8 ± 86.9 (M) 50.2 ± 55.1 (F)	–	–	–		Jiang et al. (Chap. 12)

(continued)

Table 36.1 (continued)

Regions	Ratio of migrants (%)	Migration distances[a] (km)	Home range size (ha)			Site fidelity		Factor of migration	References
			Summer	Winter	All year	Summer	Winter		
Mt. Fuji	90.9 ($n = 11$)	–	–	–	259.6 ± 127.5 (M) 147.5 ± 59.9 (F)	–	–	Snowfall (autumn)	Ohba (Chap. 13)
Kinki	37.8 ($n = 45$)	3.6 ± 1.6(M) 4.3 ± 2.1(F)	–	–	384(M) 201(F)	–	–	Snowmelt (deciduous forest)	Yokoyama et al. (Chap. 14)
Shikoku	0 ($n = 6$)	–	–	–	43(M) 53(F)	–	–		
Kyushu	10.1 ($n = 69$)	3.8 ± 0.2(M) 7.0 ± 5.3(F)	–	–	154(M) 137(F)	–	–		

[a] Migration distance was measured on a straight line between the seasonal ranges
[b] F denotes female deer
[c] UM denote upward migrants (Igota et al. 2004)
[d] DM denote downward migrants (Igota et al. 2004)
[e] NM denote non-migrants (Igota et al. 2004)
[f] M denotes male deer

seasonal movements. However, sika deer inhabiting the southern area migrated only 3–4 km in Kinki and 3–7 km in Kyushu (Table 36.1). Small migratory distances of 3.6 ± 2.5 (SD) km ($n = 9$) have also been reported in Kyushu (Yabe and Koizumi 2007), but winter habitats were not fixed as they were used as temporary snow shelters (Chap. 14).

According to the latitudinal gradient, these migration patterns and distances reflect the vegetation type of the northern deciduous broad-leaved forest and southern evergreen broad-leaved forest. The phenological differences between deciduous broad-leaved forests, which show distinct seasonal changes, and evergreen broad-leaved forests, which are seasonally stable, are related to the seasonal stability of the home range and nutritional condition of deer combined with winter severity.

Climate and Season Effects

Eighty-two percent of the collared deer were migrants in the inland Tohoku region. However, only 12.5% of deer migrated seasonally in coastal areas (Chap. 9, Table 36.1). The climate patterns regarding snowfall are quite contrasting between the Japan Sea (western) side and the Pacific (eastern) side of the archipelago because of the westerlies and the warm Tsushima Current in the winter (Yabe and Takatsuki 2009), respectively. The typical climate pattern is seen in the Tohoku region of northern Honshu and Hokkaido, where snow accumulates 2–3 m or more (Rikiishi et al. 2004). Therefore, sika deer living in the mountainous areas (inland) of the Tohoku region migrate to the coastal zone where resident deer are found (Chap. 9). Southern Hokkaido has less snow and a larger population of sedentary deer, so the pattern is likely similar to that in the coastal area of Tohoku (Chap. 8).

The timing of the spring migration occurs between March and April and is related to snow melting (Chaps. 8, 9 and 10), while a departure from their wintering area occurs in February in the Tanzawa region (Chap. 12). A previous study reported that the onset of spring migration coincided with the loss of snow cover (Uno and Kaji 2000; Igota et al. 2004; Takii et al. 2012), increase in temperature (Takii et al. 2012), and forage availability (Igota et al. 2004). Autumn migration is triggered by snowfall and low temperatures in the Kirigamine Highland, central Japan (Chap. 10; Takii et al. 2012). In the Kinki and Kyushu areas, deer that inhabit the evergreen broad-leaved forests are sedentary (Chap. 14), whereas deer that prefer deciduous broad-leaved forests are migrants escaping from deep snow (Chap. 14). These results suggest that snow is the primary factor affecting sika deer migration.

High site fidelity to the summer home range became apparent in the various sika deer habitats (Table 36.1). Most deer monitored for ≥ 2 seasons had overlapping summer and winter home ranges (Chaps. 10 and 11). The distance between the centers of activity (COA) of successive winter home ranges was greater than that of successive summer ranges (Chap. 10). The high fidelity to the summer range corresponds to earlier studies of sika deer (Uno and Kaji 2000; Igota et al. 2004) and other cervids, white-tailed deer (Tierson et al. 1985), and mule deer (Brown 1992; Nicholson et al. 1997). Uno and Kaji (2000) proposed that the reasons for the relatively lower fidelity to winter ranges were the annual changes in forage availability, winter severity (e.g., snow depth), and logging activity in the winter season.

Differences in Sex and Age

In the Tanzawa Mountains, male deer tended to travel longer distances than female deer (Chap. 12) although the sample size of GPS-collared male deer was insufficient to assess sex differences in migration patterns. In Shizuoka Prefecture, central Honshu, the seasonal migration of adult males in areas with little snow occurs between the breeding season (September–November), suggesting that adult males migrate to areas with more females (Chaps. 13 and 15). Sika deer in the Oze area migrated about 26 km, crossing the border of Gunma and Tochigi Prefectures (Chap. 11). Seasonal movement across county borders has also been reported between Yamanashi and Shizuoka Prefectures (Chap. 13).

Dispersals of young deer were observed in two regions: a juvenile (1–3 years old) male and a fawn female in the Tanzawa area (Chap. 12), and four juvenile (12–23 months old) males in the Kirigamine area with dispersal distances ranging from 3 to 40 km (Chap. 10). Few studies have reported sika deer dispersal in Japan (Maruyama 1981; Kaji 1988; Yamazaki and Furubayashi 1995). Yamazaki and Furubayashi (1995) reported one 2.5-year-old male dispersed from his mother's range in the Tanzawa area. Most mammalian species exhibit male-biased dispersal and female philopatry (Greenwood 1980). We found that juvenile males of sika deer tend to disperse in the same manner as the northern cervids, such as red deer (Haanes et al. 2011), white-tailed deer (McCoy et al. 2005), and roe deer (Anderson et al. 1998). However, Jiang et al. (Chap. 12) reported that one fawn female was a disperser. Kaji (1988) also reported that a young female deer dispersed 80 km, and the dispersal of females contributed to the expansion of the summering population in eastern Hokkaido. Dispersal of young females has also been observed in mule deer (Garrott et al. 1987) and white-tailed deer (Nelson and Mech 1992). We need more information on dispersals to understand the expansion and change in the spatial-temporal deer population structure.

Implication for Management

More movement patterns and home range studies should be performed because the sample sizes of GPS-collared male deer were insufficient to evaluate sex differences in these chapters. Okumura et al. (Chap. 11) and Yokoyama et al. (Chap. 14) surveyed the vegetation types included in the deer home range; however, the other studies did not analyze the habitat sufficiently. Today, we can obtain plenty of high-resolution location data using GPS tools. Sika deer are distributed throughout Japan and live in various habitats, including subarctic conifer forests in Hokkaido, deciduous broad-leaved forests in northern Japan, evergreen broad-leaved forests in the southern area, and areas with subalpine vegetation at high elevations (Chap. 3). The Japanese archipelago not only has diverse vegetation but also has various terrains. Plant productivity and phenology vary widely among these habitats, and sika deer are adapted to various habitats. Researchers should study the habitat use and habitat preferences of sika deer using GPS telemetry in the future. Managers can use these data for efficient population, habitat, and ecosystem management. In the northeastern part of Japan, where the distribution of deer is expanding, the use of GPS may be helpful for identifying their home range and developing culling strategies to maintain low densities (Chap. 13). Researchers and managers should cooperate and share the GPS location data as Tachiki and Yoshida proposed, similar to the concept of “SikaBase” (Chap. 8) and “Eurodeer” (Cagnacci et al. 2011, https://eurodeer.org/).

36.1.2 Food Habits

The food habits of sika deer have been characterized as below; the northern sika deer are the grazer type depending on the presence of dwarf bamboos and other graminoids. In contrast, the southern sika deer are browsers depending on the availability of browse and fruits, which largely corresponds to their genetic groups and vegetation zones (Takatsuki 2009). On the other hand, sika deer are considered “intermediate feeders” among cervid species with very flexible food habits because of their advanced and efficient fiber digestion (Hofmann 1985). This would be expected in primitive deer from warmer climates, with well-defensive floras (Geist 1998). Sika deer can survive using poor-quality resources (Chaps. 17, 18 and 30), because they utilize most plant species, except for a small portion of unpalatable species (16%) out of 843 species (Hashimoto and Fujiki 2014). Furthermore, when sika deer faced severe food limitations, they used litterfalls and unpalatable plants as alternative resources for degraded habitats (Chap. 16, Nakahama et al. 2020).

36.1.3 Population Growth Pattern

The increased pattern of sika deer abundance shows high plasticity depending on habitat quality. If habitat conditions are good, populations can grow faster. For example, forest edges created by forest fragmentation have a positive effect on the pregnancy rate of females (Miyashita et al. 2008). Artificial grasslands where fertilized grasses are planted provide high-quality food for the sika deer and frequently used by sika deer excepting winter (Iijima 2018a), and high nutrient foods such as fertilized grasses increase their body mass, leading to higher pregnancy rates and younger reproduction (Hata et al. 2021). As a result, the population growth rate and carrying capacity of sika deer are higher in habitats with higher proportions of artificial grasslands (Iijima et al. 2013; Iijima and Ueno 2016).

In contrast, sika deer can persist in poor habitat conditions. Although sika deer show clear food preferences (Hashimoto and Fujiki 2014; Iijima and Otsu 2018), they can change their food depending on availability (Chap. 16). They can eat litterfalls as their staple food, which contributes to maintaining a high-density deer population as reported on Nakanoshima Island (ca. 50 deer/km^2; Chap. 17), Tanzawa Mountains (>20 deer/km^2; Chap. 18), and Yakushima Island (>100 deer/km^2; Chap. 19). The plasticity of feeding behavior of sika deer is higher than that of other deer species (Chaps. 30 and 31). For these characteristics, the survival rate of adult female sika deer remains high even under high-density conditions (Ueno et al. 2018). However, the survival rate of fawn sika deer drastically decreases under high-density conditions (Ueno et al. 2018), as well as the pregnancy rate of female yearlings (Chap. 7). Consequently, the population growth of sika deer is regulated by density dependence (Chap. 5), and the strength of density dependence differs according to food conditions (Chap. 17; Iijima and Ueno 2016). However, these density-dependent effects occurred at high density or close to the carrying capacity. Thus, sika deer are considered to be the most highly evolved K-selected species. Therefore, although the regulation of access to favorable habitats effectively reduces population growth, the density of sika deer will be kept high by food switching, and the recovery of vegetation will never be accomplished unless intensive population management focuses on sika deer (Chaps. 16 and 17).

Recent advances in spatially explicit harvest-based modelling (Chap. 4; Iijima 2020) made it possible to estimate the spatiotemporal dynamics of deer abundance. By estimating sika deer abundance on a spatially fine scale, various factors such as population control, landscape components, and climate conditions on population growth can be examined. In Japan, population management of sika deer is conducted by prefecture units, and the target population abundance is also set at prefecture units (Iijima 2018b). However, such a social management unit may differ from a biologically meaningful unit (Chap. 35; Apollonio et al. 2010), and the size of a prefecture may be too large as a management unit. To promote population management by effective management units, the estimation of sika deer abundance and the response to hunting and culling pressure by spatially fine scales are mandatory. For example, Iijima et al. (2013) showed that the proportion of hunted and culled deer and its effectiveness on population control greatly differed among 5 km square grid cells in Yamanashi Prefecture. If a region where hunting and culling pressure is not sufficient to reduce the sika deer population is clarified, the manager can then notice the necessity of increasing the number of hunted and/or culled deer (i.e., feedback management; Chap. 32; Kaji et al. 2010).

Ueno et al. (Chap. 5) showed that sika deer abundance is affected by the proportion of various landscape components and temperature. Landscape components differ greatly among locations for human activity. Because sika deer move long distances to search for favorable habitats (Part II), the effect of landscape components on the population growth of sika deer should be clarified. Further, effective population management requires demographic and genetic monitoring of deer populations and adaptive management changes to the management unit system in response to monitoring results (Chap. 35).

36.2 Impact on Ecosystem

36.2.1 Vegetation

Impact on Vegetation

The rapid expansion of deer range and the increase in deer abundance on a nationwide scale (Chap. 2) have affected the vegetation in all vegetation zones (warm temperate zone, cool temperate zone, subalpine zone, alpine zone) along with secondary vegetation (Chap. 3). In evergreen broad-leaved forests in southern Japan and deciduous broad-leaved forests in northern Japan, overgrazing causes a decline in shrub-layer vegetation (shrub and herbaceous layer) and decreases species numbers. The compositional and structural changes associated with increasing deer density in cool-temperate forests showed a consistent pattern as the dwarf bamboo disappeared, available browse cover disappeared, bark stripping of palatable species increased from small to large trees, and unpalatable plants expanded (Chap. 16).

The shrub-layer decline rank (SDR) indicates decline of shrub-layer vegetation in a stand due to sika deer and is correlated with the relative population index and several variables that indicate the status of certain components of forests (Chap. 36; Fujiki et al. 2010). Thus, shrub layer status is a key factor for maintaining forest ecosystems, mitigating soil erosion, maintaining soil properties, and retaining nitrogen for ecosystem functions (Chaps. 23 and 27). Furthermore, it indirectly affects aquatic environments, suggesting linked impacts on terrestrial and aquatic ecosystems (Chap. 27).

In northern Japan, the dwarf bamboo (*Sasa* spp.) is a densely covered understory in deciduous broad-leaved forests and is an important winter food source because of its abundance, stable availability (evergreens), utilization by the deer, and tolerance to grazing (Takatsuki 1983). In the northern forests of deciduous broad-leaved forests, such as Nakanoshima Island in Hokkaido (Chap. 17), the Tanzawa Mountains in Kanagawa prefecture (Chap. 18), and the Ashiu Research Forest in Kyoto (Nakahama et al. 2020), deer became dependent on fallen leaves after the elimination of the dwarf bamboos. In the evergreen broad-leaved forests of Yakushima Island, the dependence on litterfall as a food source increased with increasing deer density above 20 deer/km^2, which resulted in a nonlinear relationship between deer density and deer feeding pressure (Chap. 19). Litterfall contributes to the maintenance of a high-density deer population and prevents vegetation recovery in the previously mentioned areas as well as in New Zealand forests (Chap. 31).

Under chronic deer herbivory, the vulnerable forbs disappear aboveground via deer grazing, and they can seldom form soil seed banks but are invulnerable forest forb species can form soil seed banks (Chap. 26). This mechanism can explain why chronic overbrowsing reduces the number of species in the seed bank faster than ground vegetation (Shinoda and Akasaka 2019), and the damage to vegetation seemed to have accumulated belowground and resulted in further decreases in ground vegetation and soil compaction (Chap. 24).

Why Does Vegetation Not Recover in Habitats under Long-Term Chronic Overgrazing, Even at Low Densities?

In the cool-temperate zone, deciduous broad-leaved forests in Tanzawa, Kanagawa Prefecture (Chap. 33), secondary forests in Boso Peninsula, Chiba Prefecture (Chap. 24), and Hyogo Prefecture (Chap. 34), vegetations have been affected by intense deer foraging for a long time. In these areas, the recovery of understory vegetation has not progressed despite low deer density through intensive population control. The following five main factors are cited as reasons for this:

1. Food habit plasticity (Chaps. 17, 18 and 30).
2. Palatable plant species disappear aboveground and seed banks (Chaps. 24 and 26).
3. Unpalatable plants occupied and prevented the recovery of original vegetation (Chaps. 25 and 33).
4. Slow recovery of shrub-layer vegetation (Chap. 34).
5. Extreme darkness resulting from socioeconomic changes in secondary forests (Chap. 24).

Coomes et al. (2003) suggested the following examples of situations in which deer impacts may not be reversible based on a literature review: (1) palatable species remaining highly browsed even at low deer densities as a result of diet switching; (2) occupation of vacated niches by plant species not eaten by deer; (3) local extinction of seed sources; (4) fundamental alterations to successional pathways; (5) shifts in ecosystem processes; (6) other exotic animals becoming naturalized and weakening the effectiveness of single-species control; and (7) exotic plants weakening the effectiveness of single-species control.

Tanentzap et al. (2009) tested whether a 92% reduction in the population of invasive non-indigenous red deer in New Zealand and the maintenance of their population at a low density (<2 deer km^2) for nearly four decades led to the recovery of deer-preferred species. They suggested three reasons why deer impacts may not be reversible: (1) the low growth rates of species in New Zealand, (2) density-dependent diet switching by deer, and (3) altered successional trajectories and belowground processes.

Factors (1) to (5) by Coomes et al. (2003) and (1) to (3) by Tanentzap et al. (2009) are almost the same, which correspond to factors (1) to (4) by the former that explain the irreversible changes in vegetation after reduction of deer in Japan. Sika deer have more remarkable dietary plasticity, resulting in a more significant impact on ecosystems than other deer species. Thus, the high herbivory pressure of sika deer and the dark forest floor are the main factors preventing the recovery of vegetation (Chap. 24). It has been pointed out that the history of the relationship between deer and the forest determines whether the vegetation returns to its original state after the deer has been reduced (Nuttle et al. 2014; Tanentzap et al. 2012; Mysterud 2006, Chap. 24).

36.2.2 Interspecific Competition

Interspecific food competitions between sika deer and other ungulates have been reported both within and outside the original range of sika deer. In the south of the Russian Far East, sika deer can displace other ungulate competitors from their preferred habitats and, in high numbers, have a serious impact on vegetation (Aramilev 2009). In the British Islands, sika deer shift diets to obtain the most nutritious food available at any given time in a given place, which might lead to their densities being higher in suitable habitats than those of other species (Chap. 29). In New Zealand, sika deer are widely sympatric with red deer (*Cervus elaphus*), but the sika have largely displaced red deer from many parts of that range (Chap. 31; Banwell 2009), with a greater impact on the ecosystem relative to red deer because of their presumed better ability to digest poor forage (Fraser 1996; Husheer et al. 2006). Similarly, sika deer have more remarkable dietary plasticity in the USA and are more successful in degraded habitats, where sika deer outcompete white-tailed deer (Feldhamer and Demarais 2009). Changes in niche breadth and diet quality in favor of sika deer, as well as the dietary overlap between the two species, strongly indicate a dietary competition between sika deer and white-tailed deer (Chap. 30).

There was evidence of interspecific competition via overlap in resource use between the sika deer and red deer in England (Chap. 29) and sika deer and white-tailed deer in the Delmarva Peninsula, USA (Chap. 30). However, no evidence exists on the influence on the population dynamics of both species. Direct competitive effects in terms of population dynamics might occur under severe resource limitation, which favors sika deer, but might be prevented by population control (Chap. 29) or high habitat quality (Chap. 30).

In central Japan, sika deer and Japanese serow (*Capricornis crispus*) inhabited sympatrically, and although vegetation has been reduced due to high densities of sika deer, the serow population has not yet been threatened (Chap. 28). The impact of sika deer on Japanese serow populations needs to be carefully monitored.

36.2.3 Ecological Community

Sika deer carcasses, which were abandoned after they were killed by hunting or culling, are a large high-quality food resource for many vertebrate scavengers. They may impact individual and population levels in a variety of ways (Chap. 21). An increase in the deer population has a positive effect on providing food resources (i.e., dung) to some dung beetles but has negative effects for other dung beetles as the deer change the vegetation and soil properties through browsing, which is likely to degrade the dung beetles' habitat conditions. Thus, the response of dung beetles to the changes in deer density is highly complex (Chap. 22). The impact of deer on insect communities is a complex process that occurs at both the individual and population levels. Clarifying the impact of each process and selecting an appropriate spatiotemporal scale in line with the research objectives are necessary to understand the general trend of the interaction (Takagi 2017).

36.3 Future Challenges for Research and Management

36.3.1 The Role of Humans in Ecosystem Management: Toward a Shrinking Society

In the introductory chapter, we described that historically, humans hunted sika deer as natural resources and culled deer as pest animals to prevent agricultural damage. Humans have modified landscapes as users of ecosystems since the Edo period. On the other hand, modern agriculture and forestry, which developed when deer density was low after the fuel revolution in the 1960s, did not require wildlife damage control techniques and relied on hunters to cull the nuisance animals that occasionally caused damage. As a result, animal damage prevention was not an integral part of agriculture and forestry, and the resource value of deer meat and fur was lost.

Since natural regulation of sika deer cannot be expected to restore vegetation (Chaps. 17 and 19), intensive population control has been conducted in the World Natural Heritage Sites of Shiretoko (Chap. 32) and Yakushima Island (Chap. 19). In the Ashiu Research Forest (Chap. 27), various forestry production activities have been conducted since the Edo period, such as charcoal making, burning for thatch, and deforestation until the end of 1980 (Field Science Education and Research Centre, Kyoto University 2021). Damage to vegetation by deer became apparent in the late 1990s (Chap. 27) when forest use and hunting declined.

The paradigm shift in wildlife management policy from natural regulation to artificial management can also be seen in the Yellowstone National Park. Since the 1970s, the Yellowstone National Park has adopted a policy of natural regulation in response to natural processes (predation, weather, habitat conditions, etc.). However, since the mid-1990s, a population management plan has been adopted to artificially reduce ungulate populations by 50–90% to restore key vegetation resources (Plumb et al. 2014). This policy shift is based on the recognition that for thousands of years before the establishment of the Yellowstone National Park, biodiversity was richer than it is today due to hunting and burning by Native Americans (Yonk et al. 2018; Mosley and Mundinger 2018).

Currently, most plantations have reached their harvest period in Japan; however, the presence of sika deer, which damages planted trees, is a major obstacle to the clear-cutting and reforestation of plantations. Thus, removing sika deer with home ranges around plantations, reducing labor costs, and ensuring the effective management of protective fences are important steps to reduce feeding damage caused by the sika deer (Chap. 15).

To restore the resilience of heavily damaged forests by the sika deer, intensive population control to reduce deer density and promote habitat management by installing fences in the forest gap is required for 10–30 years depending on the forest type and extent and duration of damage (Chaps. 16 and 25). Natural forest recovery following plantation clear-cutting could be inhibited even at relatively low deer densities of 4–6 deer/km^2 if a major source of regenerated trees is the non-Fagaceae trees (Fujiki and Sakata 2021). Because palatable species are vulnerable aboveground and in seed banks to deer herbivory, conservation measures by the deer-proof fence are needed when the organs of the plant remain aboveground (Chap. 26) or before population management succeeds (Chap. 20). In addition, forests subjected to chronic foraging are vulnerable to external shocks (typhoons and clear-cutting); therefore, integrated forest and deer management practices are needed (Chap. 25, Fujiki and Sakata 2021).

Considering the depopulation in Japan, creating compact cities for aggregate rural landscapes and setting the transition zone between human settlements and depopulated land are proposed as the land-sharing approaches for efficient wildlife management (Tsunoda and Enari 2020). Furthermore, restoration of wolves to maintain mountain forest ecosystems has been proposed (Tsunoda and Enari 2012; Sakurai et al. 2018). However, if the wolves expand their distribution, a new problem arises: who will manage them? Different strategies should be applied for different management units for wolves by responsible political entities (Mech 2017), but such management is not accomplished even for sika deer in Japan (see Sect. 36.3.2). The reintroduction of wolves requires a system to manage the wolf population using guns, whose ownership is strictly limited by law in Japan. Studies in other regions where deer species and wolves exist revealed that the effect of predation by wolves rarely regulated deer population growth (Vucetich and Peterson 2004; Vucetich et al. 2005) or rarely contributed to the degraded vegetation recovery from deer (Winnie 2012).

Since ecosystems cannot be maintained and restored without human intervention, it is necessary to build a social ecosystem in a shrinking society. To achieve this, in addition to restructuring land use, including abandoned land, it is necessary to establish a comprehensive approach and a system to maintain biodiversity, agriculture, and forestry through the sustainable use of deer, with humans as users (drivers) of ecosystems and deer as valuable components of ecosystems.

36.3.2 Importance of Integration of Multiple Data for Evidence-Based Policymaking

Managers must decide on the management plan, although there are many uncertainties about deer abundance and the ecological and social impact of sika deer. Then, the management plan should be based on scientific evidence (Pullin and Knight 2003) and NOT political power. For evidence-based policymaking, various monitoring data on sika deer should be gathered and analyzed. However, sika deer management is managed separately in the different sectors of the Japanese government. For example, sika deer abundance is managed by a sector that focuses on wildlife population management (e.g., the Ministry of Environment), and the impact of sika deer browsing on planted trees are managed by a sector that focuses on forest management (e.g.. the Ministry of Agriculture, Forestry and Fisheries). However, the intensity of the impact of sika deer on vegetation is higher in areas with high sika deer density (Iijima and Nagaike 2015) and in areas surrounded by certain landscape types (Takarabe and Iijima 2020). The usage of a certain place by sika deer differs seasonally because of their movement (Part II). Information about deer management, such as sika deer abundance, vegetation, landscape components, and movement, should be integrated into a common platform.

Currently, deer management needs to be considered not only for vegetation conservation but also for human health. Drivers of this problem are due to changes in land use, and similar problems occur in Europe (Apollonio et al. 2010). Deer vehicle collision (DVC) is a direct threat to human health (Chap. 32). Furthermore, sika deer are also parasitized by tick species (Yamauchi et al. 2009), and the ticks on sika deer may carry infectious diseases such as tick-borne encephalitis (Mansfield et al. 2009); Lyme disease (Brett et al. 2014), Japanese spotted fever (Mahara 1997), severe fever with thrombocytopenia syndrome (SFTS) (Yun et al. 2014; Wang et al. 2015), and Yezo virus syndrome (Kodama et al. 2021). The relationship between host and tick is complex because ticks have three developmental stages (i.e., larvae, nymphs, and adults), and tick parasite hosts vary depending on their developmental stages (Randolph 2004). However, because sika deer expand their distribution in Japan (Chap. 2) and their body size is relatively large among Japanese mammals, the increase in sika deer may contribute to the increase in ticks and the risk of tick-borne diseases (TBD). Matsuyama et al. (2020) showed that the number of patients with Japanese spotted fever correlated with sika deer density. Therefore, preventive population management of sika deer may decrease the risk of TBD, in addition to the prevention of crop damage and ecological impact. However, the DVCs are managed by a sector about traffic (e.g., the Ministry of Land, Infrastructure, Transport, and Tourism) and the surveillance of zoonosis and the number of patients are managed by a sector about public health (e.g., the Ministry of Health, Labour and Welfare). Therefore, the integration of data on sika deer contributes to the effective prevention of risk to human health.

Fortunately, rapid advances in digital technology have made it easy to store data digitally and share it on the web. In the wake of the African swine fever that raged in Europe, the ENTWILD project, founded by the European Food Safety Authority (EFSA), is organized to collect comparable data at the European level to analyze the risks of diseases shared between wildlife, livestock, and humans (https://enetwild.com/). Recently, the "European Observatory of Wildlife" (https://wildlifeobservatory.org/) was started as one of such web platforms that deal with monitoring data of mammals in Europe through the project ENTWILD. At the same time, advances in statistical modeling make it possible to treat these big data in a single framework. A web interface that can overlay various information and provide these data publicly will contribute to advances of actual management of sika deer.

36.3.3 Management Unit and the Role of the Land Manager

Setting a Proper Management Unit

In Europe and North America, sport hunting is a major tool for population control and resource management, where a target harvest number is assigned to game areas or wildlife management units. In Japan, hunting follows a licensing system, which has been liberalized, and there is no quota system or any official requirement to apply for a permit to enter the land. Currently, in addition to hunting, subsidized culling by local hunters is a major tool used for population control. Thus, the concept of management unit (MU) systems has not been clearly defined, and many management programs by prefectures establish management zones based on social requirements rather than the demographically independent MU (Chap. 35). Because population control of overabundant deer is a major management goal in Japan, wildlife managers need to establish proper MUs based on the biological population ranges, and management entities should correspond to the spatial scales of MUs.

There is an increased importance for MUs because of urban deer (Honda et al. 2018). Deer in urban areas may cause DVC and carry vectors of zoonosis. However, the use of guns in urban areas is prohibited in Japan, and the lethal control of urban deer is difficult. Because bold deer tend to explore new habitats, population control around urban areas is important, and the setting of MU in such regions should be considered.

Management Entities that Respond to Spatial Scales

Sika deer migrate seasonally across the administrative boundaries of municipalities and prefectures and are distributed continuously (Sect. 36.1.1). Population management is conducted based on the “Specified Wildlife Conservation and Management Plans” established by each prefectural government (Iijima 2018b); however, more enlarged management policies and plans are needed because of seasonal migration and movement and distribution across the boundaries of prefectures. Therefore, when implementing population management, it is necessary to consider the habitat conditions in neighboring municipalities and prefectures.

The deer have been culled as part of nuisance control by municipalities and population control by prefectures. However, the management of spatial jurisdiction and the roles and responsibilities of each municipality and prefecture are not clearly defined. To address this issue, municipalities should prioritize nuisance control, and population control by prefectures should be conducted in cooperation with the relevant municipalities under the subsidiarity principle (Kaji 2020).

In Japan, wild animals are defined as res nullius or people having no property rights over them until they are killed. Therefore, there is no direct relationship between land ownership and deer management. Hunting is principally free so that hunters can enter anywhere for hunting, except for places where hunting is generally prohibited, such as wildlife sanctuaries, temporary hunting prohibited areas, and places where owners have restricted access. Hunting is also allowed in public lands, such as national forests unless hunting restrictions exist. However, these public land managers do not have official responsibility for deer management.

In the future, cooperation among agriculture, forestry, and nature conservation sectors in Japan will be required to integrate the management of highly plastic sika deer in all land-use interests to clarify the management entities and their roles according to the landscape of backwoods, Satoyama, urban areas, and areas of expanded distribution, such as cooperative deer management among land managers, scientists, and hunters in Pennsylvania (Stout et al. 2013). For this purpose, experts with specialized knowledge and skills in science-based wildlife management should be educated and trained at universities, and a system should be established in which municipalities assign wildlife countermeasures staff, and prefectural governments assign wildlife management experts to work together with officials in charge of agricultural and forestry policy (Science Council of Japan 2019). Such experts in governments can bridge the gap between scientists and public officers and promote science-based deer management. To successfully manage the highly plastic sika deer in a shrinking population society, a wide range of data should be integrated, and decision-making should be based on evidences from these data.

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