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# The Japanese Macaques

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# The Japanese Macaques

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*Front cover*: *Upper*: An elderly female macaque grooming her long-time grooming partner of the same age in Katsuyama. Photo by Masayuki Nakamichi. *Center left*: An adult female and her infant feeding on the fruit of *Viburnum dilatatum* on Kinkazan Island. Photo by Naofumi Nakagawa. *Center middle*: An adult female feeding on new leaves of *Zelkova serrata* in spring on Kinkazan Island. Photo by Yamato Tsuji. *Center right*: An adult female carrying her infant on her back on Kinkazan Island. Photo by Naofumi Nakagawa. *Lower*: Macaques grooming and resting in a lowland forest on Yakushima Island. Photo by Shigeru Suzuki.

*Back cover*: *Upper*: Macaques resting in a tree on a snowy evening in the southwestern part of the Shimokita Peninsula. Photo by Shiro Matsuoka. *Center left*: Macaques sitting in the waters of a hot spring in Shiga Heights. Photo by Minoru Kinoshita. *Center middle*: An alpha male sided by two estrus females, one a full-grown adult (*right*), the other an adolescent (*left*), in the southwestern part of the Shimokita Peninsula. Photo by Shiro Matsuoka. *Center right*: An adult female feeding on the fruit of *Swida macrophylla* in autumn on Kinkazan Island. Photo by Naofumi Nakagawa.

*Spine*: A mother and her newborn infant in the southwestern part of the Shimokita Peninsula. Photo by Shiro Matsuoka.

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# Preface

The first sightings of Japanese macaques (*Macaca fuscata fuscata*) were made in 1948 by two Japanese students – Jun'ichiro Itani and Shunzo Kawamura – who were led by Kinji Imanishi, then a lecturer at Kyoto University. They spotted a group of wild Japanese macaques at Cape Toimisaki, Miyazaki Prefecture, while doing field research on feral horses. The behaviors of the macaques seemed more interesting to them than did those of the horses. This first impression motivated them to visit Koshima Islet, 150 m offshore and about 10 km from Toimisaki, to assess the islet as a site for field research on macaques. On December 3, 1948, they searched for the macaques on Koshima but never saw them. Nevertheless, Itani considered that day to be the beginning of the first studies on Japanese macaques in Japan (Itani 1991). In the 60 years or more that have passed since then, field studies on Japanese macaques have made considerable progress along with Japanese primatology. In addition, there have been some milestone achievements, such as the founding of the Japan Monkey Centre in 1956, which launched *Primates,* the first international journal of primatology; the establishment of the Primate Research Institute, Kyoto University, in 1967; and the organization of the Primate Society of Japan in 1985 (for details, see Chap. 1 by Yamagiwa). Numerous articles on the fruitful outcomes of these undertakings have been published in international scientific journals (e.g., *Primates*); furthermore, a number of books on the subject have been written in Japanese, such as the two bibles for Japanese field primatologists, *Takasakiyama no Saru* [The monkeys of Takasakiyama] (Itani 1954) and *Nihonzaru no Seitai* [Ecology of Japanese macaques] (Kawai 1964). Surprisingly, however, until now there has been no book published in English that features the broad range of field research on Japanese macaques at various study sites.

To commemorate the 23rd Congress of the International Primatological Society to be held at Kyoto in 2010, we have created a book comprising two types of contributions: chapters and topics. The chapters are fascinating reviews by specialists in each genre of field primatology; this section systematically presents the knowledge on Japanese macaques accumulated for some 60 years. All the chapters focus in varying degrees on intraspecific variation, which makes this book unique in field primatology. By contrast, the topics introduce each contributor's recent work on Japanese macaques from very distinctive approaches, which come not only from the contributor's own genius but also from the knowledge accumulated by previous researchers. Some parts of this section are brief summaries of published works, while others are preliminary reports of work that has not been published.

The field data from various study sites enabled us to make interpopulation comparisons (for entire map of Japan, see Fig. Ia; for study sites, see Fig. Ib). These sites included the northern limit of the distribution of Japanese macaques, the Shimokita Peninsula (41°N); its southern limit, Yakushima Island (30°N); and its nearly highest limit, Mt. Yarigatake (3,180 m above sea level [a.s.l.]) (Izumiyama 2002). Table I summarizes the general information collected at 11 long-term field research sites on Japanese macaques (for locations, see Fig. Ib). The mean minimum temperature drops to –15°C and snow depths exceed 2 m in January at Shiga Heights, 1,480 m a.s.l. (36°N) (for details, see also Chap. 2 by Hamada and Yamamoto and Chap. 5 by Tsuji) (for photos, see color plates). The vegetation within the range of Japanese macaques is roughly classified into two groups: cool-temperate deciduous broad-leaved forests in the north, and warm-temperate evergreen broad-leaved forests in the south (see Chap. 5 by Tsuji) (for photos, see Fig. II). Owing to human encroachment, the degradation and loss of forests results in crop raiding by the macaques (see Chap. 7 by Muroyama and Yamada). We call this category the crop-raiding macaques (group) in this volume. In other areas, local governments and private companies run “monkey parks” where the staff provides free-ranging groups of macaques with foods such as sweet potatoes, wheat, and peanuts to enable tourists to see the macaques easily. We call this category the provisioned macaques (group). A third category, which subsists only on foraged food resources, we call simply wild macaques (group) (for photos of these three types of macaques, see color plates).

The most suitable target for intraspecific socioecology is the Japanese macaque, living in such varied environments. Thus far, primate socioecology has aimed to elucidate the ecological determinants of social structure and the mating system, and has developed through the method of intragenera and interspecies comparison (Wrangham 1980; van Schaik 1989; Isbell 1991; Sterck et al. 1997). This approach leads to an understanding of social adaptation of the species to past environments under phylogenetic constraints. Now is a fitting time to put great emphasis on understanding intraspecific variations in social structure and the mating system. Intraspecific variations may provide evidence of social adjustment of the species to the current environment (Henzi and Barrett 2003; Chapman and Rothman 2009).

In broader genres of field studies other than socioecology, intraspecific variations – including behavioral, physiological and morphological ones – that occur in response to temporal change in the environments in the absence of genetic changes are known as phenotypic plasticity. Carroll and Corneli (1999) schematically explain phenotypic plasticity in contrast to alternative causes. We often observe a difference in the mean value of a phenotypic trait between two populations of the same animal species inhabiting different environments (Fig. IIIa). The environments could include physical elements, such as temperature and snowfall, or ecological factors, such as vegetation type, food abundance, and predation pressure. The difference in the mean phenotype would be attributable to environmental differences, and individuals in two populations would show the same mean phenotype

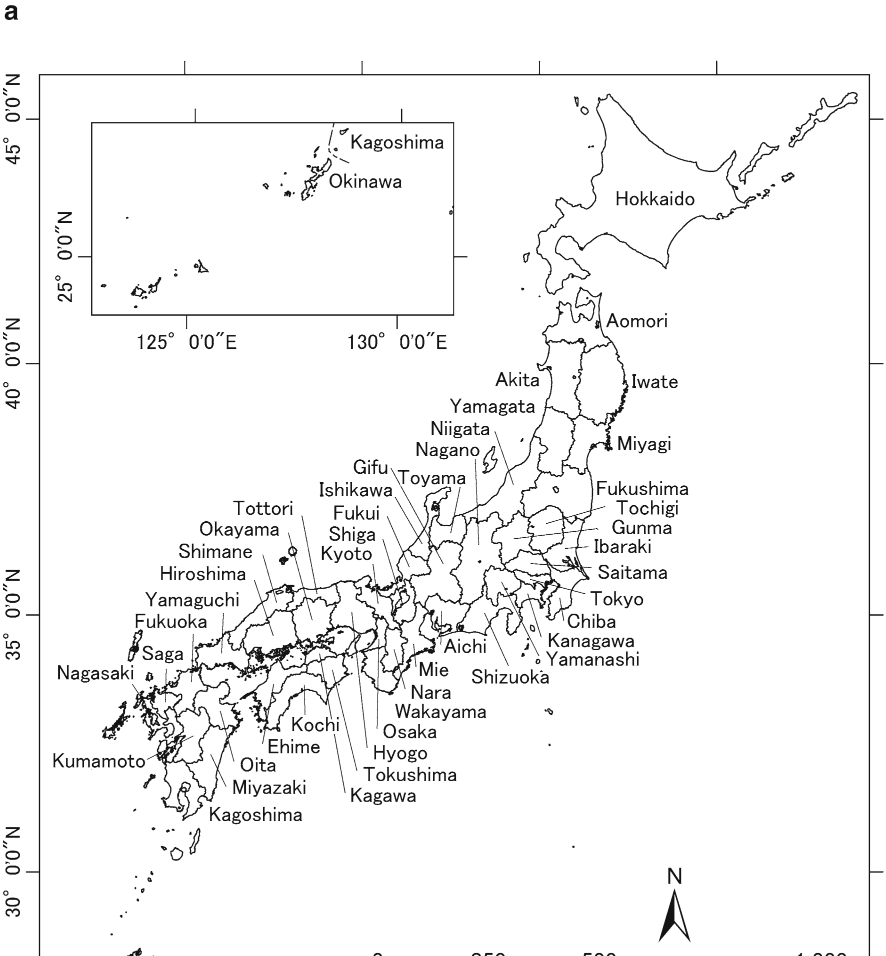

**Fig. I** Maps of Japan. (**a**) The entire map of Japan with names and boundaries of prefectures. *Inset:* Okinawa Prefecture, the southernmost part of Japan. (**b**) Locations referred to in this book. *Open circles* Eleven long-term field research sites of Japanese macaques; *closed circles* other study sites of Japanese macaques; *arrows* other sites. The maps of Japan are from *Boundary data of cities, towns and villages of Japan ver. 6.2* by ESRI Japan Corporation, used with permission

when observed under identical environments (Fig. IIIb). On the other hand, approximate genetic differences are found even among populations of a species with gene-flow restriction. If the interpopulation differences are based on genetic differences (i.e., genetic determination), then the differences would be maintained for a short

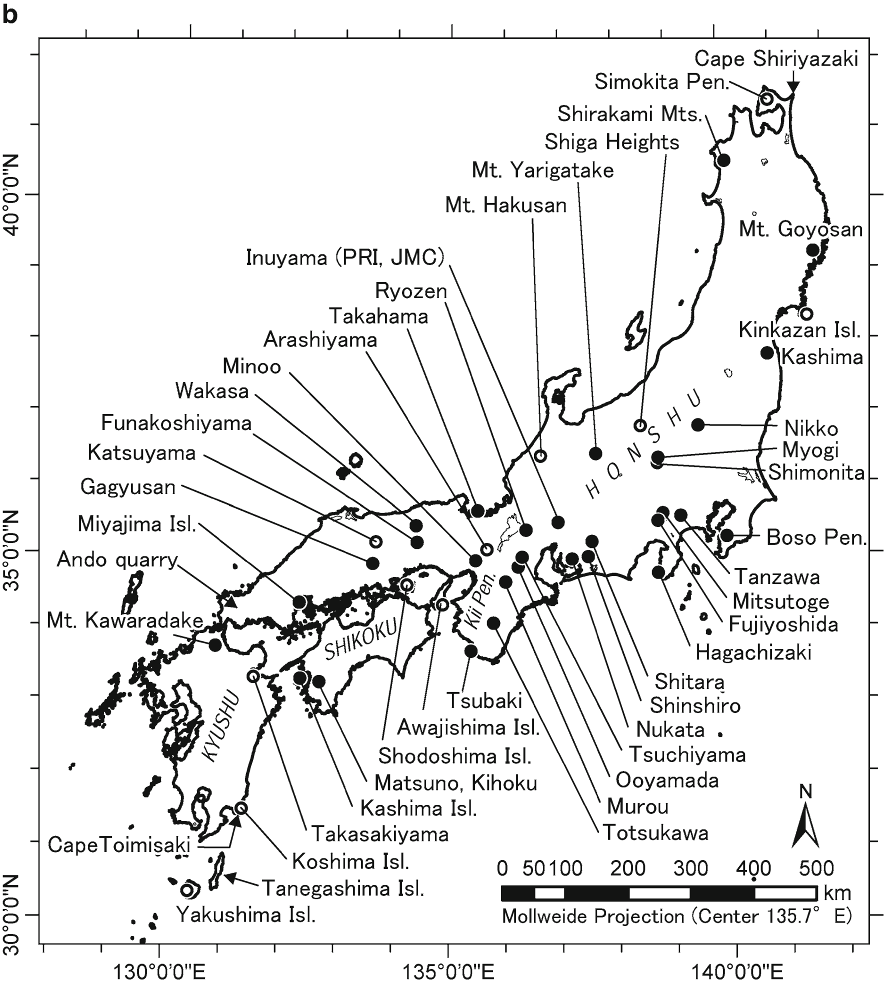

**Fig. I** (continued)

duration irrespective of the environments (Fig. IIIc). The third possibility is a combination of these two. Mean phenotypes depend on the environment in a different way in each population ("reaction norm," de Jong 1995). The upper population exhibits greater phenotypic plasticity than does the lower (Fig. IIId). Note that the reaction norm per se is based on genetic background. In addition, behavioral primatologists focus on the proximate mechanisms that form phenotypic behavioral plasticity: tradition via social transmission, or not.

A comparison of the provisioned groups of Japanese macaques with the unprovisioned ones of the same groups enables us to find astonishing plasticity. For example, high-quality, abundant food supplied by humans increased the birth rate

**Table 1** Summary of 11 long-term field research sites

| Name (Prefecture) | Conditions | Year of first research | Duration of provisioning | Long-term study period | Vegetation type[a] | Mean monthly temperature (°C) (lowest; highest)[a] | Annual precipitation (mm)[a] | Maximum depth of snow cover (cm)[a] | Days per year on which snow cover reached 10 cm | Sources for research history[b] | Sources for meteorological information |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Shimokita Peninsula (Aomori) | Provisioned, crop-raiding, wild | 1952 | 1964–1976 | 1963 to present | Deciduous broad-leaved forest | 9.7 (–0.9; 21.6) | 1259.3 | 75 | 77.8 | Izawa (1981), Izawa and Nishida (1963) | Japan Meteorological Agency, Wakinosawa (1979–2000) |
| Kinkazan Island (Miyagi) | Wild | 1962 | – | 1982 to present | Deciduous broad-leaved forest | 11.4 (0.9; 23.5) | 1064.5 | 17 | 5.1 | Izawa (2009) | Japan Meteorological Agency, Ishinomaki (1971–2000) |
| Shiga Heights (Nagano) | Provisioned, crop-raiding, wild | 1960 | 1962 to present | 1960 to present | Deciduous broad-leaved forest | 10.5 (–1.4; 23.6) | 1450.3 | 223 | 119.3 | Suzuki (1965), Wada (1979), Kutsukake (2000) | Japan Meteorological Agency, Nozawaonsen (1979–2000) |
| Hakusan (Ishikawa) | Provisioned, crop-raiding, wild | 1964 | 1966–1995 | 1968 to present | Deciduous broad-leaved forest | 12.6 (1.3; 24.7) | 2840.5 | 113 | 71.2 | Izawa (1982), Hayashi (1998) | Japan Meteorological Agency, Hakusan-Yoshino (1979–2000) |
| Arashiyama (Kyoto) | Provisioned | 1954 | 1954 to present | 1954 to present | Evergreen broad-leaved forest | 15.6 (4.6; 27.8) | 1545.4 | 6 | 0.4 | Hazama (1964), Koyama et al. (1992) | Japan Meteorological Agency, Kyoto (1971–2000) |
| Awajishima Island (Hyogo) | Provisioned | 1973 | 1967 to present | 1978 to present | Evergreen broad-leaved forest | 15.3 (5.0; 26.3) | 1457.4 | 3 | 0.2 | Nakamichi et al. (1983, 1997) | Japan Meteorological Agency, Sumoto (1971–2000) |
| Shodoshima Island (Kagawa) | Provisioned | 1953 | 1953 to present[c] | 1953 to present[c] | Deciduous broad-leaved forest | 15.3 (5.1; 26.6) | 1128.9 | – | – | Yamada (1966), Zhang and Watanabe (2007) | Japan Meteorological Agency, Uchionomi (1979–2000) |
| Katsuyama (Okayama) | Provisioned | 1958 | 1958 to present | 1958 to present | Evergreen broad-leaved forest | 13.4 (2.1; 25.6) | 1455.3 | 18 | 2.5 | Itoigawa (1973, 1997) | Japan Meteorological Agency, Tsuyama (1971–2000) |
| Takasakiyama (Oita) | Provisioned | 1950 | 1952 to present | 1950 to present | Evergreen broad-leaved forest | 16.0 (6.0; 26.8) | 1677.8 | 2 | 0.1 | Itani (1954), Kurita et al. (2008) | Japan Meteorological Agency, Oita (1971–2000) |
| Koshima Islet (Miyazaki) | Provisioned | 1948 | 1952 to present | 1952 to present | Evergreen broad-leaved forest | 17.9 (8.5; 27.2) | 2598.4 | 0 | 0 | Itani and Tokuda (1958), Watanabe et al. (1992) | Japan Meteorological Agency, Aburatsu (1971–2000) |
| Lowland of Yakushima Island (Kagoshima) | Wild | 1952 | – | 1975 to present | Evergreen broad-leaved forest | 19.2 (11.4; 26.9) | 4358.7 | 0 | 0 | Maruhashi (1980), Takahata and Yamagiwa (2000) | Japan Meteorological Agency, Yakushima (1971–2000) |

[a] See also Chap. 5 by Tsuji

[b] See also Chap. 1 by Yamagiwa

[c] Five groups were provisioned during 1953–1961. Only one of them is still provisioned as of 2010. Studies have been conducted intermittently since 1953

**Fig. II (a, b)** Cool-temperate deciduous broad-leaved forests on Shimokita Peninsula. (**c, d**) Warm-temperate evergreen broad-leaved forest on Yakushima Island. (Photographs by N. Nakagawa. (**a, b**) November 2008; (**c, d**) November 2006)

and infant survival rate (see Chap. 11 by Nakamichi and Yamada) and consequently increased the group size to a maximum of 1,255 at Takasakiyama (Sugiyama and Ohsawa 1988). It is in provisioned groups that social transmission of newly acquired behaviors, such as sweet potato washing and stone handling, were found among individuals (see Chap. 9 by Huffman et al.). In this sense, provisioned groups can be referred to as "experimental groups living in the wild," which highlight the potential plasticity of Japanese macaques. Ironically, the recent invasion of the macaques into human settlements also reveals their high behavioral plasticity (Chap. 7 by Muroyama and Yamada). Comparisons of translocated groups of macaques and those in original habitats also provide ample grounds for behavioral plasticity. Chap. 8 by Koda and Sugiura shows that Yakushima macaques change the acoustic features of their contact calls according to the acoustics of their translocated habitat. By contrast, the morphological characteristics observed in the interpopulation difference – such as body size, tail length, and lightness of pelage color that suitably correspond to Bergman's, Allen's and Gloger's rule (see Chap. 2 by Hamada and Yamamoto) – are supposed to be based on genetic background.

Generally, however, it is difficult for field primatologists to identify whether the fundamental cause of observed interpopulation behavioral differences is phenotypic plasticity, genetic determination, or a combination of both. In the strict

**Fig. II** (continued)

sense, difficulties of identifying the cause might hold true even for what we call "adaptation" to environment in diet (Chaps. 4 by Hanya and 5 by Tsuji; Topic 3 by MacIntosh and Huffman), activity budget (Chap. 5 by Tsuji), and female proceptivity (Chap. 10 by Fujita).

It is hoped that accumulated knowledge not only of phenotypic traits but also of genetic factors (see Chap. 3 by Kawamoto and Topic 1 by Inoue-Murayama et al.) and environmental factors will help us to address such a challenging issue. In Chap. 12, for example, Nakagawa questions the idea that youngest ascendancy was the product of provisioning, which was deduced from a comparison of a wild group in Yakushima with provisioned groups. Nakagawa attributed the lack of youngest ascendancy in Yakushima macaques to genetic determination.

All contributors provided high-quality papers despite time constraints and other demands made upon them. Two contributors, Drs. Yoshi Kawamoto and Miho

**Fig. II** (continued)

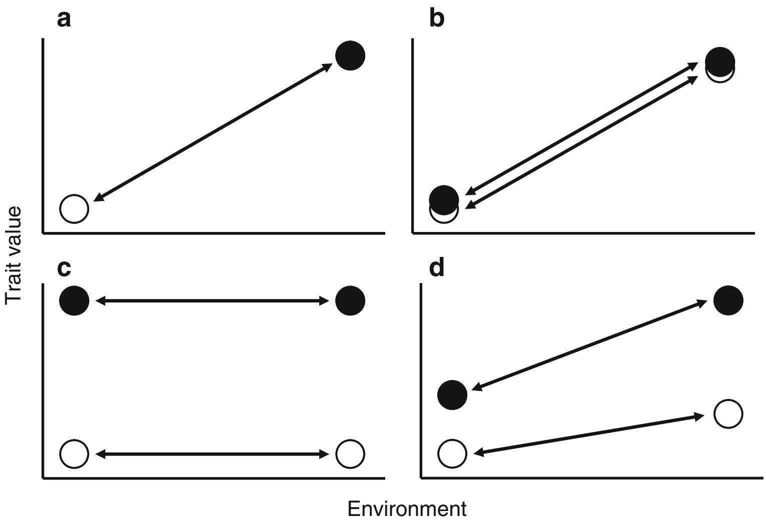

**Fig. III** Three different interpretations of observed interpopulation variations in a phenotypic trait. (**a**) Observation. (**b**) Phenotypic plasticity. (**c**) Genetic determination. (**d**) A combination of phenotypic plasticity and genetic determination

Inoue-Murayama, were also willing to help us to review the papers. Two series editors, Drs. Juichi Yamagiwa and Tetsuro Matsuzawa, and five anonymous reviewers provided useful comments and heart-warming encouragement for the creation of this volume. Ms. Aiko Hiraguchi, Mr. Kaoru Hashimoto, and Ms. Fumiko Yamaguchi of Springer Japan provided us with unfailing support and constant help throughout the production of this book. Every contribution to this volume is the result of the great efforts of many people – staff members of the "monkey parks," the officials of local governments, local citizens, technicians, students, and researchers. We, the editors of the book, NN, MN, and HS, enjoyed our graduate courses under the guidance of Profs. Masao Kawai and Yukimaru Sugiyama, Kyoto University; Prof. Naosuke Itoigawa, Osaka University; and Prof. Ken'ichi Aoki, The University of Tokyo; respectively. We are very grateful to all the above-named individuals.

We hope our readers will enjoy this book about Japanese macaques by Japanese contributors for people all over the world!

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# Color Plates

## Regional variations from the north to the south

**1** Macaques walking through the snow in the southwestern part of the Shimokita Peninsula. Photo by Shiro Matsuoka.

**2** Macaques feeding on ears of rice in a swidden field in the northwestern part of the Shimokita Peninsula. Photo by Katsuya Suzuki.

**3** An adult female feeding on the fruit of *Viburnum dilatatum* on Kinkazan Island. Photo by Naofumi Nakagawa.

**4** Macaques sitting in the waters of a hot spring in Shiga Heights. Photo by Minoru Kinoshita.

**5** Three infant macaques resting on the branch of a tree in Hakusan. Photo by Minoru Kinoshita.

**6** Macaques aggregated in a pattern of distributed food forming the Japanese word *saru* (“monkey”) on Awajishima Island. Photo by Toshikazu Nobuhara.

**7** An adult female performing stone handling behavior in Arashiyama. Photo by Masayuki Nakamichi.

**8** An elderly female grooming her long-time grooming partner of the same age in Katsuyama. Photo by Masayuki Nakamichi.

**9** Macaques in an unusually large resting cluster in Chosikei, Shodoshima Island. Photo by Peng Zhang.

**10** An unusually large group of macaques at an artificial feeding site in Takasakiyama. Photo by Minoru Kinoshita.

**11** An adult female, with her infant on her back, washing a piece of sweet potato on Koshima Islet. Photo by Takafumi Suzumura.

**12** An adult female huddling with two juveniles in a heavy rain in a lowland forest of Yakushima Island. Note the raindrops on their backs. The water-repellent hair appears to be an adaptation to an environment that receives heavy rains. Photo by Mari Nishikawa.

## Seasonal variations from spring to winter

**13** A mother and her newborn infant in the southwestern part of the Shimokita Peninsula. Photo by Shiro Matsuoka.

**14** Macaques feeding on flowers of Yoshino cherry (*Prunus x yedoensis*), with Sika deer (*Cervus nippon*) gleaning the remains below them on Kinkazan Island. Photo by Takeharu Uno.

**15** An adolescent male foraging for seaweed on the coast of Kinkazan Island. Photo by Takeharu Uno.

**16** Juvenile males playing in the sea on Koshima Islet. Photo by Takafumi Suzumura.

**17** Macaques grooming and resting in a lowland forest on Yakushima Island. Photo by Shigeru Suzuki.

**18** A full-grown male Yakushima macaque (*Macaca fuscata yakui*) in a lowland forest on Yakushima Island. Photo by Juichi Yamagiwa.

**19** An adolescent female copulating with an adult male in the southwestern part of the Shimokita Peninsula. Photo by Shiro Matsuoka.

**20** An alpha male sided by two estrus females, one a full-grown adult (*right*), the other an adolescent (*left*), in the southwestern part of the Shimokita Peninsula. Photo by Shiro Matsuoka.

**21** An adult female holding her infant and being sided by her juvenile, in heavy snow in Shiga Heights. Photo by Minoru Kinoshita.

**22** Macaques feeding on dormant buds of *Morus australis* in a snowfall in the southwestern part of the Shimokita Peninsula. Photo by Shiro Matsuoka.

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# Part I

# Intra-specific Variation: Overview of Field Research and Related Studies

# Chapter 1: Research History of Japanese Macaques in Japan

**Juichi Yamagiwa**

## 1.1 Scope of Japanese Primatology in the First Stage

Japanese primatology is characterized by a unique history among mammalian studies in Japan. In general, mammalogists initiated their studies by collecting specimens from the point of view of systematics, morphology, and physiology, and then investigated the adaptive significance of these traits from the aspect of ecology. In contrast, the Japanese primatologists initiated their studies with sociological perspectives. After World War II, Kinji Imanishi, based in the Department of Zoology, Kyoto University, started his field studies on feral horses (*Equus caballus*) at Cape Toimisaki in Miyazaki Prefecture. The aim of his study was to understand the species society and to thus trace the evolution of human society (Asquith 1991, 2000; Takasaki 2000). The concept of species society had developed from his study on mayflies skittering around the river in Kyoto and extended to all living things (Imanishi 1941). He began to consider the evolution of animal societies, and in particular, the evolution of human society through comparisons with other animal societies (Imanishi 1951a).

During a survey on feral horses at Toimisaki in 1948, his students Jun'ichiro Itani and Shunzo Kawamura encountered a group of wild Japanese macaques (*Macaca fuscata fuscata*; Fig. 1.1). Although it was very brief, they were impressed by this encounter and expected a more complex social structure to be present in macaques than in horses. Thus, they decided to study Japanese macaques and formed the Primate Research Group in 1951. They searched extensively for good study sites for Japanese macaques in their natural habitats in Japan. However, the Japanese macaques were very shy and were frightened away from encounters with human observers as a result of past hunting and chase pressures from the farmland

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**Fig. 1.1** Pioneers of Japanese primatology at Cape Toimisaki in 1950. From *left* to *right*: Shunzo Kawamura, Kinji Imanishi, Kisaburo Tokuda, and Jun'ichiro Itani. (From Itani Jun'ichiro Archive of Primate Research Institute, Kyoto University)

inhabitants. Kawamura and Itani tried to habituate macaques by provisioning (feeding them with sweet potatoes, wheat, or soybeans) and finally succeeded in provisioning at Koshima Islet (Miyazaki Prefecture) and Takasakiyama (Oita Prefecture) in 1952.

Imanishi conducted field studies on feral horses by identifying each individual and naming it. He thought this method to be essential for illustrating social interactions among individual animals. The Japanese primatologists used this method to study Japanese macaques and, later on, other primate species. Individual identification by marking had previously been used by Clarence R. Carpenter for rhesus macaques (*Macaca mulatta*) at Cayo Santiago Island. Instead of using artificial marks, the Japanese primatologists identified each macaque by features and body characteristics (shape, color, scars). The first generation of Japanese primatologists thought that social structure was not merely a reflection of individual survival or reproductive strategies but reflected a norm of species-specific sociality (Itani 1972, 1985). To elucidate the social features of primates, Imanishi devised a guide to field studies by (1) adopting methods of comparative sociology, (2) basing work on individual identification, and (3) recording social interactions from prolonged continuous observations (Imanishi 1951b, 1957).

Daily observations on social interactions among Japanese macaques at the artificial feeding sites produced many findings. The social structure of Japanese macaques is based on multimale–multifemale group formation with linear dominance rank, a leadership system, and matrilineal kin relationships (Itani 1954; Kawamura 1958; Kawai 1964).

Females acquire their dominance rank via two rules: (1) a daughter is dominant to all females who are subordinate to her mother and (2) maturing daughters become dominant to their older sisters, a process termed youngest ascendancy (Kawamura 1958). Correspondingly, females belonging to the same kin-group outrank females of other kin-groups, and dominance rank among mature sisters correlates inversely with age. Dominance relationships between individuals often reflect their affiliative relationships to the third party who is dominant to both of them (Kawai 1958). After provisioning, the group size rapidly increased, and the large group consisting of more than 100 individuals split into several groups everywhere (Sugiyama 1960; Furuya 1960). The increased conflicts between matrilineal kin-groups with increasing group size may have caused group fission, and after such separations males associated with kin-groups unrelated to them (Koyama 1970).

Another important finding induced by provisioning was the "culture" of Japanese macaques. A young female started to wash sandy potatoes with freshwater in a stream near an artificial feeding site at Koshima a few years after provisioning. Then, she began washing potatoes and wheat with seawater (Fig. 1.2). These newly acquired techniques were transmitted to other group members. Kawamura (1959) and Kawai (1965) called such sharing a subculture or preculture, and traced the process of transmitting such information. Other than feeding techniques, conspicuous local variations were found in paternal care (Itani 1963a) and in some vocalizations

**Fig. 1.2** Washing potatoes with seawater at Koshima Islet. (Photograph by Noritsugu Yamaguchi)

in close proximity (Itani 1963b). Imanishi (1957) and Itani (1991) regarded such variations in subtle behavior as behavioral culture in Japanese macaques.

Detailed observations on social interactions among macaques led to various findings of their complex social perceptions. Mori (1975) found local variations in vocalizations emitted in grooming requests. Affiliative interactions among solitary males and alliance formations in conflicts within groups have been reported (Sato 1977; Watanabe 1979; Sugawara 1980). Mother–son relationships, along with development (Norikoshi 1974) and dominance relationships in extraordinary large groups with provisioning (Mori 1977), have been described and analyzed from the point of view of social organization of Japanese macaques. Sociosexual behavior and changes in sexual partnership through copulation were analyzed in relationship to individual life history (Hanby et al. 1971; Hanby and Brown 1974; Enomoto 1974, 1978; Takahata 1980, 1982). These findings suggested that higher dominance rank did not always lead males to mating success, but that their past relationships with females or their choice of females might affect their success. It was suspected that provisioning may have influenced such relationships and choices.

## 1.2 Field Studies of Japanese Macaques in Their Natural Habitats

Provisioning Japanese macaques stimulated not only research interests but also the tourism industry in Japan. Oita City has conducted provisioning of Japanese macaques with researchers from the beginning, and opened the Monkey Park at Takasakiyama to attract tourists who could observe macaques at close range. This new business was very successful. The Japanese macaques and their social life were introduced in newspapers, journals, films, and television programs, and many tourists visited Takasakiyama, paying the entrance fee for monkey watching. By 1977, the number of monkey parks with provisioned Japanese macaques available for tourism had increased to 37 in Japan (Nihonzaru Editorial Committee 1977; Fig. 1.3).

However, provisioning appeared to have a great influence on the life of Japanese macaques. The annual rate of increase in group size at Takasakiyama after provisioning was 1.102, which meant that group size doubled every 7 years (Masui 1976). Irrespective of location, without exception group size increased after provisioning, and tended to exceed 100 individuals after prolonged provisioning (10–20 years) (Nihonzaru Editorial Committee 1977). Provisioning improved the nutritional condition of Japanese macaques and increased survival rates and birth rates, especially for dominant-class females (Sugiyama and Ohsawa 1982). Daily travel distance decreased, and the ranging of the macaques concentrated on the artificial feeding sites. Their activity time budget for feeding and moving decreased and that for resting and for social interactions thus increased. Agonistic interactions may have increased at the artificial feeding sites, and such situations may have reinforced dominance relationships among group members (Wada 1979; Izawa 1982). Provisioning also

**Fig. 1.3** Provisioning of Japanese macaques at Iwatayama Monkey Park in Arashiyama

affected unprovisioned groups by male movements. The larger groups produced by provisioning stimulated more males to transfer into adjacent small groups and changed intergroup relationships (Suzuki et al. 1975; Sugiyama and Ohsawa 1982).

These findings at the artificial feeding sites led the younger generation of Japanese primatologists to study Japanese macaques in their natural habitats. From single groups observed under isolated conditions at Takasakiyama, Koshima, and Arashiyama (Kyoto Prefecture), Itani (1954) and Kawai (1964) concluded that all males sought dominant social status within a group and that the losers left the group to become solitary males. However, as observations on male immigration and emigration increased in various habitats where several groups overlapped their ranges, it became obvious that males usually leave their natal groups before maturity. They transfer into other groups and do not stay for a prolonged period, even after taking the highest rank (Sugiyama 1976). It began to appear likely that several small multimale–multifemale groups in partly overlapping ranges might represent the natural population structure (Kawanaka 1973). In 1952, just before provisioning at Koshima and Takasakiyama, Kawamura and Itani visited Yakushima Island, Kagoshima Prefecture (the southern limit of distribution) and estimated such a social structure as consisting of several groups for Japanese macaques (*Macaca fuscata yakui*) from fragmentary observations and information from hunters (Itani 1952). However, because of the success of provisioning, Japanese primatologists did not choose Yakushima as their study site. If they had continued their intensive field studies at Yakushima, they could have easily found such social structure in which males frequently transferred between groups. It was only in the mid-1970s that the younger generation of Japanese primatologists started to conduct field studies

**Fig. 1.4** Japanese macaques in the warm-temperate forest at Yakushima Island

in the natural habitats of Japanese macaques everywhere in Japan without provisioning.

However, it was difficult to habituate Japanese macaques in their natural habitats because of their shyness and the dense undergrowth in deciduous forests. Researchers started to follow the fresh trails of macaques on the snow. They could observe macaques on the snow, but stayed at considerable distance, and observations were limited to winter. Only two places were found to satisfy the conditions for observations. Subtropical and warm-temperate forest at the low altitude of Yakushima is characterized by poor undergrowth, and visibility is high (Fig. 1.4). Their high density and small home ranges meant that it was easier to find the macaques there than in other areas. The western side of Yakushima was declared a national park in 1964, and it is not inhabited by local people. Young primatologists, including high school teachers and university students, formed research groups and conducted a census voluntarily in the early 1970s (Iwano 1983). Tamaki Maruhashi started habituation of a group of Japanese macaques without provisioning in 1975, and I joined him to habituate three groups in 1977 (Maruhashi 1980; Yamagiwa 1985). Another good study site was Kinkazan Island (Miyagi Prefecture), which is covered by cool-temperate forest. Dense undergrowth usually reduces the visibility of macaques in the cool-temperate forest of Japan. However, because of the high density of sika deer (*Cervus nippon*) in Kinkazan, herbs and shrubs were overgrazed, and visibility was high. The small island allowed researchers to find macaques again after losing them to sight. Similar to Yakushima, this island also was not inhabited by local people, and Kosei Izawa started to conduct long-term field studies on Japanese macaques without provisioning in 1982 (Izawa 1983).

Field studies on Japanese macaques in natural habitats had been conducted mainly in snowy areas in the 1960s and 1970s. The habitats of Japanese macaques constitute the northern limit of living nonhuman primate distribution. Their morphological, physiological, and ecological features may reflect their past adaptations

**Fig. 1.5** Japanese macaques in the snow at Shiga Heights

to the coldest climate in primate habitats. The foods, feeding behavior, and activity budget of Japanese macaques were investigated during heavy snow in winter (Wada and Tokida 1981; Izawa 1982; Fig. 1.5). Several general surveys including morphology, population genetics, physiology, and ecology were conducted in various habitats, and the adaptive features of Japanese macaques to cold climates were analyzed. Uehara (1977) compared food composition of Japanese macaques among different types of vegetation and found their most common foods occurred in the cool-temperate and warm-temperate forests. He hypothesized that dietary features of Japanese macaques reflect those of their ancestors coming across the Korean Peninsula. Nozawa et al. (1975) collected and analyzed blood samples from macaques captured during the surveys and proposed the “stone-step hypothesis,” meaning that gene flow occurred by male transfers between groups similar to skipping stones on the surface of the water when we throw them. Male Japanese macaques usually leave their natal group and travel a long distance to join other groups (Hazama 1965; Nishida 1966). Nozawa et al. (1991) estimated that two local populations with an intervening distance of more than 100 km were genetically independent.

## 1.3 Prolonged Socioecological Studies in Yakushima and Kinkazan

Ecological studies on Japanese macaques were conducted in their natural habitats in the 1970s. After preliminary studies on their dietary features, activities, and ranging in snowy areas, their foraging strategies in relationship to environmental factors were analyzed in various habitats. The marked seasonal changes were found in their

**Fig. 1.6** An alpha-male of a small group in the lowland forest at Yakushima Island

daily activity rhythm (Yotsumoto 1976), and the relationship between nutritional intake and energy expenditure in individual female macaques was analyzed from the bioenergetic point of view (Iwamoto 1974, 1982). A significant correlation was found between food quality with group size, daily travel distance, and home range size in both warm-temperate and cool-temperate forests (Ikeda 1982; Furuichi et al. 1982). Takasaki (1981) found a positive correlation between their group size and home range size in both habitats, and that home range size was greater in the cool-temperate forest than in the warm-temperate forest for the same group size.

A highest density of Japanese macaques in their entire habitats was estimated at the low elevations of Yakushima (Maruhashi 1982; Iwano 1983). A preliminary survey conducted at higher altitudes found lesser density and larger ranges of macaques but a similar group size to macaques at lower altitudes (Azuma et al. 1984). As Itani had expected in 1952, we found that Yakushima macaques formed smaller groups with a high socionomic sex ratio (SSR: the number of reproductive males/the number of reproductive females within a group) and moved in smaller ranges than did Japanese macaques in other habitats (Iwano 1983; Azuma et al. 1984; Fig. 1.6). Both ecological and social factors shaping these social features were investigated and discussed (Maruhashi 1982; Furuichi 1983, 1984, 1985; Yamagiwa 1985; Oi 1988).

Habituation and long-term research with individual identification of several groups found that social features of Yakushima macaques differed from those of Japanese macaques in other habitats (Fig. 1.7a,b). In provisioned groups of Japanese macaques at Takasakiyama, Gagyusan (Okayama Prefecture), and Arashiyama, group fission occurred with large group size (more than 100 individuals), and several kin-groups of females associated with a few group males to create a new group during the nonmating season (Furuya 1960; Sugiyama 1960; Koyama 1970). At Yakushima, group fission occurred at a smaller group size, mainly by nongroup males and estrous females with their kin-groups during the mating season (Maruhashi 1982; Yamagiwa 1985). A large number of males left their groups and

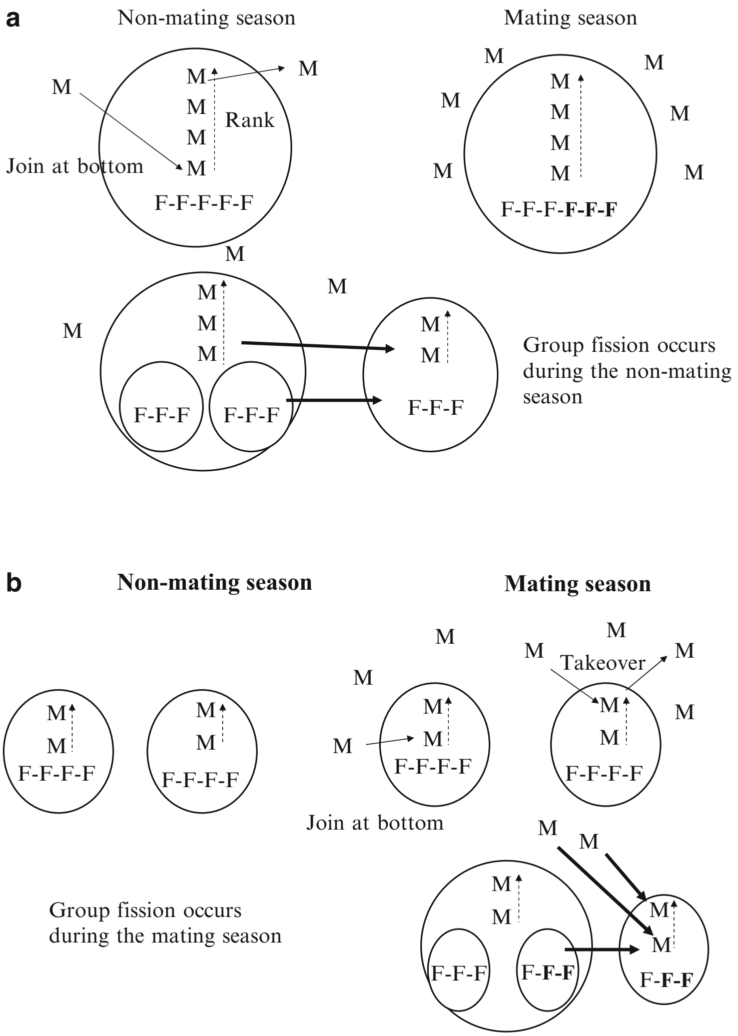

**Fig. 1.7** Individual movements and group structure of Japanese macaques based on the studies of provisioned groups (**a**), and group fissions observed in a population of Yakushima (**b**). M and F indicate adult male and female macaques, respectively. **F** An estrous female. *Solid arrows*, individual movements; *dotted arrows*, dominance ranks (from bottom to top rank)

visited other groups as nongroup males to solicit mating with estrous females during the mating season (Yamagiwa 1985; Sprague 1992). When group takeover occurred by nongroup males, females extended their estrous periods and showed strong proceptivity (Okayasu 2001). The youngest ascendancy in the dominance relationships among sisters (Kawamura 1958) was not found in the Yakushima groups (Hill and Okayasu 1995).

The population of Japanese macaques at Kinkazan was very small (a group with 60–70 individuals) when Izawa visited this island for the first time in 1962 (Izawa 1983). He found four groups with 250 individuals in 1982, when he started habituation of these macaques without provisioning. After a sudden dip of population size in 1984 as a result of poor climate and food conditions, this population has recovered rapidly through two group fissions during 10 years (Izawa 2001). Since then, a population census has been conducted by Izawa and his colleagues every year at Kinkazan. Feeding ecology was the main subject of field studies, and the optimal feeding strategy from the aspect of energetics was investigated (Nakagawa 1989a, 1990a,b; Saito 1996). Individual feeding strategies during the period of food scarcity in winter were argued based on data from Kinkazan and Shimokita Peninsula, Aomori Prefecture (Nakagawa 1989b, 1997; Watanuki and Nakayama 1993; Nakayama et al. 1999). A strong gregariousness among individuals during the cold weather, and differences in mating success between group and nongroup males, were investigated (Takahashi 1997, 2001). Differences in the social structure of the Kinkazan population from those of other populations have become apparent by these studies.

Various factors, such as climate, vegetation, provisioning, or isolated conditions, may shape the socioecological features of Japanese macaques (Yamagiwa and Hill 1998). To identify such factors, we formed working groups to compare socioecological features of Japanese macaques between Yakushima (warm-temperate forest) and Kinkazan (cool-temperate forest). Food abundance, food patch density, daily travel distance, home range size, proportion of overlap between ranges of neighboring groups, population density, group size, SSR, activity time budget, reproductive parameters, frequency of intergroup encounters, antagonism of intergroup encounters, dominance relationships between groups, male emigration and immigration, and mating patterns were compared, and relationships between variables were discussed (Table 1.1). In summary, under the higher-quality and more abundant food conditions (Agetsuma and Nakagawa 1998; Maruhashi et al. 1998), the Yakushima macaques compete more severely for resources between groups than the Kinkazan macaques (Saito et al. 1998; Sugiura et al. 2000). Such competition leads to strong intergroup antagonism, which poses the risk of group extinction or a decreased birth rate of subordinate groups after a bad fruiting season (Takahata et al. 1994a,b, 1998; Suzuki et al. 1998a; Sugiura et al. 2002). Female macaques at Yakushima more positively solicit nongroup

**Table 1.1** Ecological and social features of Japanese macaques at Kinkazan and Yakushima

| | Kinkazan | Yakushima |
|---|---|---|
| *Environmental conditions* | | |
| Year of habituation | 1982 | 1976 |
| No. of study groups | 4–6 | 2–5 |
| Mean temperature | 11 | 20 |
| Annual rainfall (mm) | 1,500 | 3,000 |

(continued)

**Table 1.1** (continued)

| | Kinkazan | Yakushima |
|---|---|---|
| Forest type | Cool-temperate | Warm-temperate |
| No. of species of trees (>5 cm in DBH) | 32 | 62 |
| Density of trees (no./ha) | 180 | 2,417 |
| Density of food trees (no./ha) | 94 | 1,802 |
| Mean diameter at breast height (DBH) (cm) | 39.6 | 12.4 |
| *Ecological features* | | |
| Distance between consecutive feeding patches (m) | 151 | 70 |
| Daily travel distance (>10 h observation) (m) | 1,878 | 1,464 |
| Annual home range (ha) | 221 | 90 |
| Range overlap between neighboring groups (%) | 53 | 63 |
| Core area overlap between neighboring groups (%) | 12 | 23 |
| Population density (individuals/km$^2$) | 30 | 80 |
| Group density (groups/km$^2$) | 0.6 | 4.2 |
| Mean group size (individuals) | 48.7 | 27.1 |
| SSR (no. reproductive males/no. reproductive females) | 0.34 | 0.87 |
| Feeding time budget (%) | 54 | 31 |
| Moving and resting time budget (%) | 34 | 45 |
| Social grooming time budget (%) | 12 | 21 |
| Feeding on fruit in total feeding time (%) | 10 | 32 |
| *Reproductive parameters* | | |
| Birth rate (no. births/female/year) (%) | 35 | 27 |
| Age at first parturition (years) | 7.1 | 6.1 |
| Interbirth interval (years) | 2.4 | 2.2 |
| Survival ratio (1–3 years old) | Male < female | Male > female |
| Age to participate in reproduction (female) (years) | 6–18 | 5–14 |
| Infant mortality (within 1 year after birth) (%) | 23 | 25 |
| *Social features* | | |
| No. intergroup encounters (no./h) | 0.012 | 0.039 |
| Proportion of agonistic encounter (mating season) (%) | 15 | 64 |
| Proportion of agonistic encounter (nonmating season) (%) | 16 | 46 |
| Dominance relationships between groups | Unclear | Large group > small group |
| Sex differences in aggression | Male > female | Male > female |
| Aggression during mating season | No difference | Males are more aggressive |
| *Male life history* | | |
| Age at first emigration (years) | 4.7 | 5.3 |
| Mean length of stay after immigration (years) | 2.9 | 2.8 |
| Dominance rank at immigration | | |
| Highest | 1 | 13 |
| Middle | 2 | 1 |
| Lowest | 6 | 14 |
| Solitary male | Many | Few |
| All-male group | Many | Few |
| Copulation by nongroup male (%) | 41 | 41 |

*Source:* Primates (1998) Vol. 39(3), Sugiura et al. (2000)

males to associate with them during the mating season (Yamagiwa and Hill 1998; Okayasu 2001). Such a tendency may promote frequent male movement between groups and diverse entries, frequent group fissions by estrous females and non-group males, and frequent nonagonistic interactions among males within a group (Sprague et al. 1998; Takahashi and Furuichi 1998). As socioecology predicts, the strong intragroup competition may form female social bonds and nepotism in Japanese macaques (Nakagawa 1998).

However, although food quality and availability may explain female gregariousness and relationships, many aspects of male association and movements remain unknown (Takahashi and Furuichi 1998; Horiuchi 2005, 2007). As suggested by the recent arguments in primate socioecology (Janson 2000; Koenig 2002; Henzi and Barrett 2003), it is difficult to find clear relationships between environmental factors and social variation within primate species where the environment changes rapidly. Adding to socioecological analyses, we should consider variation in social features of Japanese macaques in relationship to their community structure, including several groups and their life history in future studies (Yamagiwa 2008).

## 1.4 New Scope of Field Studies and Conservation of Japanese Macaques

Until the present, long-term studies on Japanese macaques with individual identification have been conducted for provisioned groups at various sites in Japan. Life history parameters based on demographic data for more than 50 years have been analyzed in both Koshima (Watanabe 2003) and Takasakiyama (Kurita et al. 2008). Infant social development, parental behavior, and social relationships among adult males and females have been analyzed from long-term observations at Katsuyama, Okayama Prefecture (Itoigawa 1973, 2001; Nakamichi and Shizawa 2003; Nakamichi and Yamada 2007; Nakamichi et al. 1995). At Arashiyama, long-term behavioral observations and DNA analysis from hair and fecal samples found that male mating success relied heavily on female choice in relationship to the male's length of tenure (Huffman 1987; Takahata et al. 1999; Inoue and Takenaka 2008). Stone handling behavior (Nahallage and Huffman 2008; Huffman et al. 2008) and social object play (Shimada 2006) have also been analyzed in relationship to environmental and social factors at Arashiyama. Suckling behavior and nipple preference have been analyzed in relationship to parity at Shiga Heights, Nagano Prefecture (Tanaka 1989, 1992, 1997, 2004). Kutsukake and Hasegawa (2005) reported the mutualism among males when a turnover occurred in a provisioned group at Shiga Heights. Grooming interactions such as louse egg-handling techniques for hygienic purposes (Tanaka 1995; Zamma 2002) or as a reciprocal strategy for association (Muroyama 1991, 1996) have been analyzed and considered from observations at long-term study sites.

Intensive field studies with individual identification have also been conducted without provisioning at Yakushima and Kinkazan (Yamagiwa 2008; Izawa 2009).

A census to estimate population size, group size, and group composition has been made every year at Shimokita, Kinkazan, Hakusan (Ishikawa Prefecture), and Yakushima. Yoshihiro et al. (1999) implemented a new method at higher elevations of Yakushima, dividing each research area into grid squares of 500 × 500 m, with an observer positioned in each grid square at a fixed point. Three to six fixed observers formed a party together with a leader who tracked the macaques. This method adapted the conventional census method for unhabituated groups of Japanese macaques so that nonprofessional fieldworkers could participate. These censuses found that small groups inhabited the higher elevations with relatively high density, in spite of the cold climate (Yoshihiro et al. 1999; Hanya et al. 2003). Subsequent field studies made at higher altitudes suggest that total annual food abundance, especially fruit, was the determinant factor of density, and mature leaves constituting fallback foods may mitigate the severity of fruit scarcity (Hanya 2004a,b; Hanya et al. 2004). At Kinkazan, long-term monitoring of food resources and feeding behavior found that Japanese macaques changed their choice of foods according to large fluctuations in nut production (Tsuji et al. 2006).

The flexible feeding strategies of Yakusima macaques according to seasonal changes in availability of high-quality foods (Agetsuma 1995a,b,c; Agetsuma and Noma 1995; Maruhashi and Takasaki 1996), their feeding ecology in relationship to seed dispersal (Noma and Yumoto 1997; Yumoto et al. 1998; Otani and Shibata 2000), and vocal and behavioral communication (Mitani 1986; Tsukahara 1990; Sugiura 1993, 1998; Sugiura and Masataka 1995; Koda et al. 2008) were investigated and discussed. Based on identification of individual macaques, female reproduction, mating strategies, intergroup male movements, and life history have been studied (Sprague et al. 1996; Thomsen 1997; Takahata et al. 1998; Sprague 1998, 2004; Suzuki et al. 1998b; Soltis et al. 2001; Matsubara and Sprague 2004; Thomsen and Soltis 2004; Soltis 2004; Thomsen et al. 2006). These data on reproductive strategies of both female and male Japanese macaques in natural habitats were comparable to those in provisioned groups (Koyama et al. 1992; Itoigawa et al. 1992; Watanabe et al. 1992; Takahata et al. 1994b, 1995).

Adding to these findings, the recent scope of field studies would focus more attention on individual reproductive strategy using steroid hormones or DNA markers. By measurement of urinary and fecal steroid metabolites during the ovulation cycle, hormone profiles and reproductive features have been investigated both in captivity and in the wild (Fujita et al. 2001, 2004). Microsatellite DNA analysis and polymerase chain reaction (PCR) techniques have been used by collecting hair, fecal, or sperm samples for determination of paternity (Inoue et al. 1990, 1993; Hayakawa and Takenaka 1999; Soltis 1999), and female and male reproductive strategies have been discussed in relationship to ecological factors, group size, dominance rank, tenure, or age (Takahata et al. 1999; Soltis et al. 2001; Soltis 2002; Thomsen and Soltis 2004; Hayakawa 2008; Inoue and Takenaka 2008). DNA markers have also been used for analysis of local genetic differentiation of Japanese macaques (Hayaishi and Kawamoto 2006; Kawamoto et al. 2007a,b). Low genetic diversity among populations of Japanese macaques suggests their recent dispersion to the islands of Japan along with distribution of vegetation and ancient bottleneck effects on some isolated populations (Kawamoto et al. 2007a,b, 2008). Morphological methodologies based on skeletal and somatic specimens have been greatly improved and used for analysis of local variations in the life history of Japanese macaques (Hamada et al. 1996, 2003).

These findings on the morphological, genetic, physiological, ecological, and social features of Japanese macaques have provided useful data for the conservation of wild populations and their habitats. However, these data have not been well implemented into the policies of wildlife management by central and local governments. The main reasons were (1) a rapid increase of crop raiding by Japanese macaques everywhere in Japan and (2) the difficulty of creating appropriate measures to control them because of their highly developed social and intellectual activities. Although Japanese macaques had not been the main subject of hunting so far, their ranging area had been limited to higher mountains until the 1960s. They avoided contacts with humans, who actively chased them away from farmlands on the lower hills and plains. However, industrialization in the 1950s and 1960s led to a decline of agriculture and to a rapid decrease in the population of rural areas. Urbanization increased timber requirements for construction and accelerated deforestation. Many roads were newly constructed in macaque habitats to transport commercial goods and people between prefectures. These human activities resulted in destruction of their natural habitats and increased their access to farmlands. Wild macaques became accustomed to crops in the abandoned farmlands and to humans using the newly constructed roads through contacts with tourists, who fed them human foods. Capture of Japanese macaques to control their raiding of crops gradually increased in the 1970s, exceeded 5,000 individuals, and reached 10,000 individuals at the end of the twentieth century (see Fig. 7.3 in Chap. 7).

Since the 1970s, Japanese primatologists have organized symposiums and workshops to discuss the recent changes in the number and range of Japanese macaques and appropriate measures to keep them away from farmlands without capturing them. A number of surveys have been conducted to estimate the number of groups and their distribution (Yoshihiro et al. 1998; Watanabe 2000; Oi and Masui 2002). Various measures have been designed and applied to decrease the raiding of crops by wild macaques (Muroyama 2003; Izawa and Miyagi Research Group of Monkeys 2005). Nevertheless, it is still difficult to establish the best methods to control the macaque's destructive activities, because there are numerous variations in their behavior according to environmental conditions. Since the Primate Society of Japan (PSJ) was established in 1985, Japanese primatologists have increased their influential power on the policies and measures of the government. From the beginning, PSJ has declared a high priority for conservation of the habitat of Yakushima macaques. Its continuous efforts obtained international support and resulted in inscription of the central part of Yakushima into the World Heritage List in 1993 and in suspension of new road construction within the Heritage site at Yakushima (Yamagiwa 2008). PSJ also declared that macaques captured for raiding crops should not be provided for invasive experimental use and recommended that the Japanese government establish guidelines for experimental use of wild Japanese macaques from the aspects of conservation and animal welfare in 2000 (Primate Society of Japan 2000).

Since the 1980s, Taiwanese macaques, rhesus macaques, and long-tailed macaques have dispersed into wild populations of Japanese macaques as a consequence of the closure of monkey gardens and inappropriate management of these captive populations (Kawamoto et al. 2001, 2007a,b). These macaque species have a large influence on the wild population of Japanese macaques and on the ecosystems of their habitat. In Wakayama and Chiba Prefectures, these macaques started interbreeding with Japanese macaques. PSJ proposed that these prefectures should prevent interbreeding and has cooperated with them to capture these macaques until now (Kawamoto 2005; Kawamoto et al. 2001, 2007a,b). The Japanese government established a law for invasive alien species and included these macaques in the list in 2004. Decisions concerning capture of pest animals was transferred from the Environment Agency (currently Ministry of the Environment) of the Japanese Government to city, town, and village mayors under the guidance of prefectural governors in 1994. The Environment Agency established a new system for management and conservation of specific animals and ordered each prefecture to make a plan for its achievement in 1999. PSJ has cooperated with this action to provide a manual for prefectures.

Although we still have many problems in the conservation of Japanese macaques, understanding of the importance of Japanese macaques as our national treasure has become widespread in Japan. Ecotourism is one of the effective measures for primatologists to promote conservation of Japanese macaques and their habitats in cooperation with local people who are seeking harmonious development in local economy and conservation. The monkey parks are now rising in popularity, especially among foreign tourists. In contrast to zoological parks or safari parks, visitors can approach free-ranging macaques to enjoy direct observations of them in close proximity at the feeding sites. Feeding macaques by visitors is strictly prohibited in most of the parks. Visitors are requested to follow the rules of observation and learn many things through careful observations. Watching the monkeys, with naming of each individual, is our traditional way to understand their social life. We need to maintain such field methods not only for research work but also for promotion of ecotourism to combine with observations in their natural habitats. At Yakushima, the number of tourists has greatly increased after the inscription of World Heritage, and more than 180 professional guides take tourists for nature walks every day. However, in addition to Japanese macaques, the number of sika deer has prominently increased in the protected areas because of the prohibition of hunting, and their damage of the undergrowth vegetation by feeding has brought many endemic plant species to the danger of extinction (Yumoto and Matsuda 2006). Because of the lack of foods on the forest floor, deer follow macaques to eat foods discarded by the macaques, even the macaques feces (Nishikawa and Mochida, 2010). Management plans of wild populations of Japanese macaques should consider sympatric populations of other mammal species. Many tourists visit natural forests and come in contact with wild macaques now, sometimes trying to feed them. The risk of disease transmission from human visitors and provisioning by tourists is increasing and becoming a greater concern. To decrease such risks and to promote conservation of Japanese macaques, cooperation with local non-governmental organizations (NGOs) and local governments is particularly important. None of the conservation measures will be successful without the interest and support of the local people.

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# Chapter 2: Morphological Characteristics, Growth, and Aging in Japanese Macaques

**Yuzuru Hamada and Ayumi Yamamoto**

## 2.1 Introduction: Origin of Japanese Macaques

The Japanese macaque (*Macaca fuscata*) is one species of the genus *Macaca*, which is now distributed in lower-latitude areas in Asia, excepting the Barbary macaque (*Macaca sylvanus*, which is distributed to Northwestern Africa). The genus *Macaca* is phylogenetically close to mangabeys and baboons (tribe Papionini; Fleagle 1999), has a medium-sized stout body, and lives either arboreally or terrestrially. According to Delson (1980), the geographical evolutionary history of *Macaca* is as follows: the genus arose 7–8 million years ago (MYA) in northern Africa, and the ancestor migrated to Eurasia via the Middle East around 5–6 MYA. Although the immigrants to southern Europe remained there for a long time, all of them are considered to be close to the extant Barbary macaque, that is, a conspecific or closely related species; they became extinct several 10,000 years ago. Other populations dispersed to Asia and flourished adaptationally but, because of the paucity of fossils, their exact evolutionary history has not yet been elucidated. On the basis of the supposed macaque fossil *Macaca palaeoindicus* (2.5–3.0 MYA) from India, the genus *Macaca* migrated from the Middle East to India along the seashore (southern course). However, a northern course cannot be denied because the majority of macaque fossils excavated have been from China or northern Vietnam. In particular, fossils from Yushe, Shanxi Province (ca. 5.5 MYA) suggest that a macaque ancestor migrated from Europe via Central Asia to China and then dispersed to Southeast and South Asia (Takai 2005).

Delson (1980) proposed the following geographical evolution scenario, a southern course, on the basis of morphological characteristics, especially tail length, morphology of genitalia, and mating behavior (Fooden 1976). (1) Migration of an ancestor of macaques to India – the lion-tailed macaque (proto-*silenus*). (2) Dispersion of proto-*silenus* from India to Indochina (Southeast Asia) via Myanmar. (3) Formation of

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species groups – accumulation of variation within localities, diversification of species from proto-*silenus*, which then became the progenitors of species groups. The *sinica*-group diversified in the area of eastern India and Myanmar and the *fascicularis*-group was formed in Indonesia. (4) Speciation within each species group, which produced the 18–21 species (Fooden 1976; Groves 2001) known at present.

The seas between insular and continental Asia are shallow. In the glacial period, when the sea level lowered, islands such as Sumatra, Kalimantan, and Java were connected together and with continental Asia, forming Sundaland. Proto-*fascicularis* has rapidly expanded its range through Sundaland to continental Asia; its populations dispersed into northern areas and diversified into proto-*mulatta* or rhesus macaques (*Macaca mulatta*) by adaptation to the colder climate.

During the interglacial, the warm and humid periods in the Pleistocene, rhesus macaques dispersed to the north in China. In the course of dispersal, the northern population adapted to the habitat, from south to north, to form a geographical cline in morphology such as in tail length [range, 30–90% of the crown-rump length (CRL); Fooden 2000]. Within the Chinese rhesus, the southern population migrated to Taiwan, having a longer tail compared to those of northern China, over the eastern China Sea; they later became Taiwanese macaques (*Macaca cyclopis*). The northern population migrated to Japan through the Korean Peninsula while the sea level was lowered and Japan was connected to the continent. According to genetic analyses, fossils, and glacial records, this ancestor is estimated to have migrated to Japan around 0.43–0.60 MYA (Aimi 2002; Iwamoto and Hasegawa 1972). On the basis of genetic analysis (Smith et al. 2007), rhesus macaques ranged widely in terms of geography and had many local clusters, and Japanese macaques clustered more closely with eastern (Chinese) rhesus macaques than with western ones. Because of this, some researchers consider Japanese and Taiwanese macaques to be local forms of rhesus macaques, not being classified as distinctive species (Smith et al. 2007). However, because both Japanese and Taiwanese macaques are morphologically distinct from rhesus macaques in tail length, pelage color pattern, and body proportions, they should be considered true species.

The ancestral population of Japanese macaques expanded their range in Japan, and their fossils were excavated from 0.12 MYA in the Shimokita Peninsula (the northernmost part of Honshu Island of Japan). Japanese macaques experienced the last glacial period, the maximum extent of which occurred about 18,000 years ago, although there were no more migrants from continental Asia. Thus, successive generations of Japanese macaques have inhabited the Japanese islands for 0.4–0.5 million years and at present range from the Shimokita Peninsula (41°N) to the Yakushima Island (30°N).

Only the Yakushima population has morphological traits sufficiently distinctive from other populations (Mouri 2000; Hamada 2002) to be classified as a subspecies, *M. fuscata yakui*. Molecular phylogenetic analysis indicates that the Yakushima population has been isolated from those on other islands for 0.178 million years; lava from the Kikaishima Island eruption burned more than half of Yakushima Island, and thus the ancestor population is considered to have experienced a bottleneck (Hayaishi and Kawamoto 2006).

Insular populations other than that on Yakushima which are distributed to smaller islands (Kinkazan, Shodoshima, and Koshima) and geographically isolated localities (e.g., Boso Peninsula) are sometimes suggested to have distinctive morphology (Mouri 2000). A dichotomous variation pattern of "central versus periphery" has been suggested for Japanese macaques, on the basis of the supposed variation in frequency of genetic flow between populations. Although we expect that the history of local populations could be reconstructed from morphology, the genetic basis of morphological variation should be examined.

Japanese macaques are considered to have adapted to the climate and environment of Japan islands by the modification of their physiques and their growth and aging patterns. We examine here the Japanese macaque's adaptation.

## 2.2 Morphological Characteristics of Japanese Macaques

Although the founder ancestor of Japanese macaques (rhesus) has already adapted to cold weather, reflected by its shorter tail [30% of crown-rump length (CRL); Fooden 2000], the Japanese macaque has advanced cold adaptation (15% of CRL). However, at the last glacial maximum, ca. 18,000 years ago, populations of Japanese macaques could not have survived in northern Japan and probably retreated to the south. Most of Europe was covered by glaciers, and macaques were exterminated there. On the other hand, Japanese macaques could have escaped to the southern or coastal areas where the warmer sea current made the climate mild. The history of range shrinkage is recorded in the variation in mitochondrial DNA sequences, that is, there are sequence types of eastern and western Japanese macaques (the border is at approximately 134°E, between Okayama and Hyogo Prefectures), and the former has less variability than the latter (Kawamoto 2007).

Japanese macaques range from 30°N to 41°N in latitude with wide variability in climate and vegetation. Accordingly, Japanese macaque local populations exhibit a geographical cline in their morphology (Hamada et al. 1996a,b). Body sizes of local populations of Japanese macaques correlate with the lowest monthly average temperatures in their habitats (Fig. 2.1), which means that the zoogeographical rule in body size (Bergman's rule) is found in the Japanese macaque. Ordinarily, the rule is explained from the scaling relationship between body mass (heat production) and body surface (heat loss). When the linear dimension of body is expressed as $L$, the body mass and body surface are proportional to $L^3$ and $L^2$, respectively; the greater the size, the smaller the ratio of heat loss to heat production. Japanese macaques have developed peripheral tissues (skin and hair) for heat insulation (Fig. 2.2), which is revealed by the fact that the northern populations have denser and longer hair (Inagaki 1985; Inagaki and Hamada 1985). Thus, the scaling mechanism of heat maintenance cannot be applicable, but the body size variation is related to energy storage against food shortage in winter (Hamada 2002). This consideration is especially true for fat accumulation, in which twice as much energy is stored as when carbohydrates and proteins are accumulated. The larger the body, the more fat can be stored.

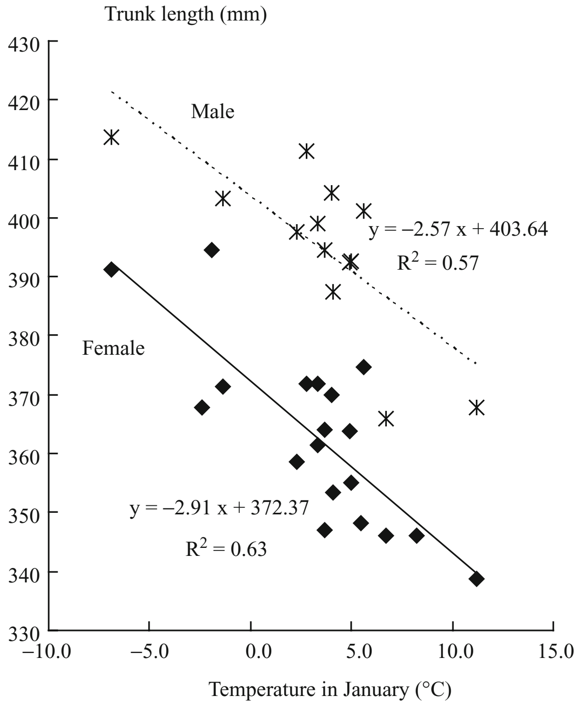

**Fig. 2.1** Body size (trunk length) in Japanese macaques and habitat average temperature in January. Macaques living in colder localities tend to be larger, which conforms to Bergman's rule (Hamada 2002)

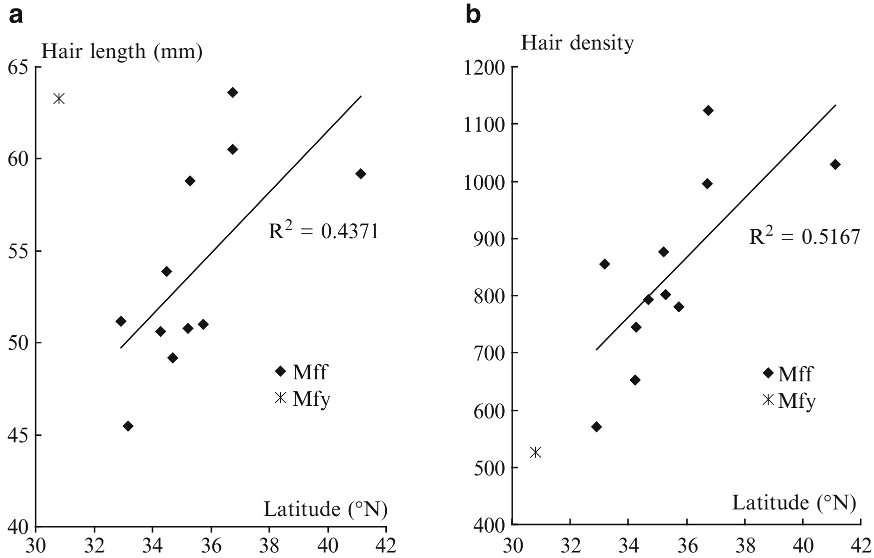

**Fig. 2.2** Geographical variation of hair length (**a**) and density, which was defined as the number of hairs counted on the 1-cm circle on skin (**b**). (Data were taken from Inagaki 1985; Inagaki and Hamada 1985)

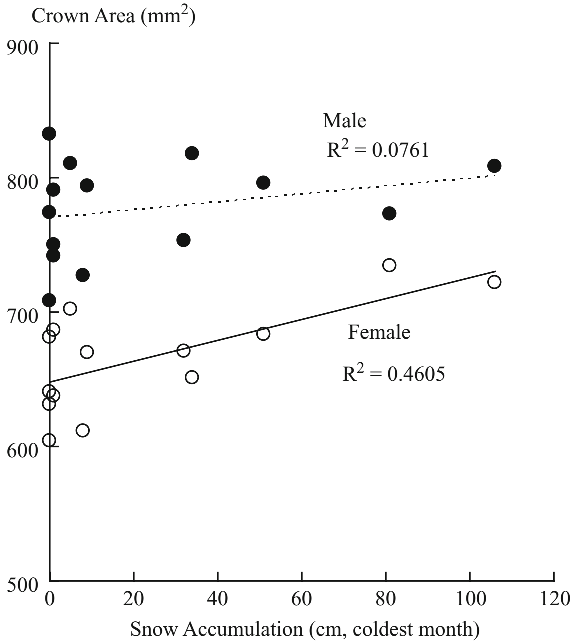

**Fig. 2.3** Relationship between dental size (molar crown area) and snowfall. *Open circles*, females; *filled circles*, males (Modified from Yamamoto 2007)

Another climate factor is the snowfall in winter. In the northern region and the Japan Sea side of Japan, snowfall prevents macaques from obtaining food. They are forced to rely on bark, which is abrasive to masticate (see Chaps. 5 and 6); thus, the molar crown area correlates with snowfall in females (Fig. 2.3; data for males insufficient; Yamamoto, in preparation). Females are not only smaller than males and thus accumulate less fat, but they must also care for infants, especially during lactation.

In general, mammal body proportion also shows a geographical cline (Allen's rule). Japanese macaque local populations exhibit a significant correlation between relative tail length and lowest monthly average temperature, that is, the macaques in northern colder localities tend to have relatively shorter tails (Fooden 1976). Pelage color variation is also clinal, conforming to Gloger's rule (Hamada et al. 1992), that is, macaques distributed in the more northern localities tend to have paler pelage (Fig. 2.4).

The morphological variability in Japanese macaques is greater and their average size is larger than those of China-derived and India-derived rhesus macaques (Table 2.1; also see Hamada et al. 1996a,b, 2005b). Sizes of Japanese macaques, represented by Arashiyama (origin from Kyoto Prefecture, caged) and Koshima (free-ranging, Miyazaki Prefecture) populations, were compared to those of Chinese rhesus macaques reared at the Primate Research Institute (PRI), Kyoto University.

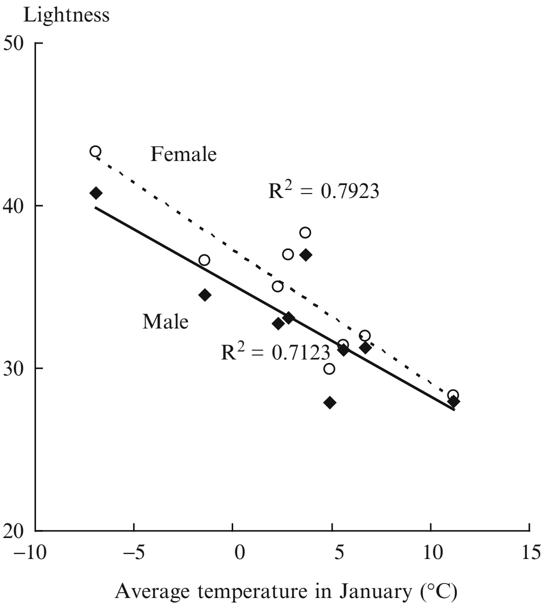

**Fig. 2.4** Geographical variation of lightness of pelage color. *Open circles*, females; *filled diamonds*, males (From Hamada 2002)

The birth dates were known for the caged macaques and the Koshima group that inhabits the islet. Koshima macaques are the smaller of Japanese macaques (Hamada et al. 1986) because of their southerly distribution. Although the insular effect could account for their smaller size, data from the insular population are not sufficient to prove this effect. Because of food scarcity, Koshima macaques are also found to have delayed growth (Mori 1979; Hamada et al. 1986). Excepting some characteristics, Arashiyama and Koshima Japanese macaques showed similar trends (Fig. 2.5, Table 2.2) as well as some differences from rhesus macaques. Japanese macaques have relatively longer facial height and upper facial height (protrusion of muzzle; length between nasal root to the midcentral maxillar incisors), but have smaller external and internal canthic breadths, meaning that their eyes are located close to each other. Japanese macaques have relatively shorter hands and fingers but greater hand and foot breadth, perhaps reflecting terrestrial foraging style and developed manipulation. The longer muzzle in Japanese macaques is an exception to Allen's rule. The rhesus macaque has a shorter muzzle in comparison with long-tailed macaques (*Macaca fascicularis*; Fooden 2000), and its shorter muzzle would be a unique characteristic.

Yakushima Japanese macaques (*M. fuscata yakui*) are classified as a subspecies on the basis of their morphological distinctiveness (craniofacial morphology; Ikeda and Watanabe 1966). Some of their morphological characteristics, such as smaller body size, relatively longer tail, and darker pelage, are explained by the geographical clines and Bergman's, Allen's, and Gloger's rules. However, they look different physiognomically and have longer hair irrespective of their more southern habitat. They also have a distinctive ear shape (the ear width/length proportion), which is found in 61% of males and in 64.6% of females in Yakushima macaques; and in about 74% of both sexes in nominotypical Japanese macaques (Hamada 2002).

## 2.3 Growth and Aging in Japanese Macaques

The rhesus macaque, which is considered to be ancestral to the Japanese macaque, ranges widely geographically from Afghanistan to China and adapts to a wide range of ecological habitat settings (weed species; Richard et al. 1989). The founder ancestor of the Japanese macaque probably migrated with the ecological and life history patterns of rhesus macaques and adapted to the habitat environment of Japan. This adaptation is of interest because comparative data have not been reported yet, and therefore we describe here Japanese macaque physical growth and aging processes.

Primates are known to have life history characteristics different from those of other mammals (Charnov 1993). Primates adopt a time strategy, meaning they grow for a longer time than nonprimate mammals and reproduce fewer offspring. Conversely, nonprimate mammals adopt an energy strategy, meaning they quickly invest energy in reproduction for their offspring to grow rapidly and reproduce greater numbers of offspring during their lives. The determining factor of primates assuming a time strategy is that they are arboreal and live in a developed society wherein they can obtain food securely and enjoy a lower risk of predation. On the basis of these factors, the mortality in adults is rather low in primates; that is, they live long lives, which is the fundamental determining factor of primates' life history characteristics.

The life stages of Japanese macaques are infantile, juvenile, adolescent, subadult, adult, and elderly, as in humans. These stages can be determined by the development of physiological functions (i.e., feeding, locomotion, reproduction, and cognition), which are common to cercopithecoids and hominoids. We examine next the life stage characteristics of Japanese macaques.

### *2.3.1 Infantile Period*

The infantile period can be demarcated by birth and onset of weaning. Intrauterine life is about 170 days in Japanese macaques, which is relatively shorter than would be expected from its body size (growth duration and lifespan scale strongly; Harvey et al. 1987). Japanese macaques are strict seasonal breeders; they mate from fall to winter and give birth from spring to summer (Nigi et al. 1980). The neonates are relatively mature even if body size influence is excluded (Hamada 1994). Infantile growth is rapid, so the infant begins to wean at 0.5 years of life (Tanaka 1992) to enter the juvenile period (but see Chap. 11). The shorter infantile period means a shorter turnover of reproduction, that is, a greater number of offspring.

**Table 2.1** Somatometric sizes of Japanese macaques and rhesus macaques (Hamada 2008)

| Measurement | Sex | Locality (Prefecture) | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Koshima (Miyazaki) | | | Takasakiyama (Oita) | | | Shodoshima (Kagawa) | | | Awajishima (Hyogo) | | | Arashiyama (Kyoto) | | | Hagachizaki (Shizuoka) | | |
| | | Average | SD | *n* | Average | SD | *n* | Average | SD | *n* | Average | SD | *n* | Average | SD | *n* | Average | SD | *n* |
| Body weight (in kg) | Female | 6.29 | 0.70 | 93 | 7.63 | 1.18 | 355 | 8.69 | 1.14 | 25 | 7.64 | 1.29 | 11 | 8.78 | 1.50 | 70 | 9.10 | 1.69 | 40 |
| | Male | 8.52 | 1.53 | 73 | 11.47 | 2.81 | 21 | 11.19 | 1.76 | 11 | 10.78 | 1.58 | 19 | 13.56 | 1.93 | 42 | 11.75 | 1.60 | 36 |
| Crown-rump L. (length, mm) | Female | 510.87 | 23.13 | 90 | 529.21 | 22.13 | 354 | 516.38 | 14.35 | 26 | 504.20 | 13.41 | 10 | 551.61 | 22.34 | 70 | 544.95 | 24.94 | 40 |
| | Male | 555.25 | 29.10 | 65 | 587.00 | 42.20 | 21 | 574.00 | 22.32 | 11 | 556.16 | 27.78 | 20 | 630.15 | 19.60 | 42 | 594.53 | 20.04 | 36 |
| Anterior trunk L. | Female | 347.72 | 17.34 | 90 | 362.81 | 18.15 | 354 | 351.54 | 17.96 | 26 | 355.30 | 9.80 | 10 | 373.38 | 18.80 | 68 | 373.25 | 17.86 | 40 |
| | Male | 376.62 | 20.33 | 65 | 394.81 | 33.93 | 21 | 390.91 | 26.27 | 11 | 384.25 | 24.98 | 20 | 430.60 | 22.67 | 42 | 400.56 | 19.25 | 36 |
| Tail L. | Female | 70.25 | 12.43 | 85 | 85.86 | 11.82 | 300 | 87.31 | 8.50 | 26 | 77.50 | 3.63 | 10 | 79.10 | 9.79 | 42 | 71.00 | 11.60 | 36 |
| | Male | 77.46 | 15.63 | 59 | 97.50 | 20.16 | 20 | 100.00 | 9.36 | 12 | 88.00 | 8.65 | 19 | 88.93 | 12.36 | 14 | 80.47 | 12.76 | 34 |
| Chest G. (girth, mm) | Female | 357.96 | 24.10 | 91 | 397.35 | 29.69 | 347 | 411.88 | 26.14 | 26 | 402.30 | 36.73 | 10 | 425.57 | 32.74 | 67 | 429.13 | 43.18 | 40 |
| | Male | 397.97 | 37.09 | 65 | 444.50 | 33.86 | 20 | 452.25 | 28.20 | 12 | 443.55 | 46.86 | 20 | 487.78 | 31.88 | 40 | 468.81 | 36.92 | 36 |
| Upper arm L. | Female | 146.08 | 5.92 | 70 | 148.25 | 6.38 | 326 | 145.69 | 7.18 | 26 | 142.91 | 6.56 | 11 | 153.98 | 6.57 | 65 | 155.08 | 5.23 | 40 |
| | Male | 160.49 | 8.75 | 53 | 167.24 | 14.23 | 21 | 166.58 | 10.64 | 12 | 159.90 | 7.44 | 20 | 176.26 | 8.58 | 27 | 172.25 | 8.88 | 36 |
| Forearm L. | Female | 151.84 | 5.78 | 70 | 155.80 | 8.46 | 326 | 150.85 | 12.51 | 26 | 150.09 | 3.86 | 11 | 157.98 | 7.43 | 65 | 165.75 | 9.09 | 40 |
| | Male | 168.57 | 9.42 | 54 | 171.71 | 13.32 | 21 | 173.75 | 12.98 | 12 | 168.53 | 8.45 | 19 | 181.26 | 12.54 | 27 | 183.97 | 9.78 | 36 |
| Hand L. | Female | 102.88 | 4.95 | 70 | 104.12 | 6.10 | 321 | 89.00 | 7.91 | 25 | 103.56 | 3.21 | 9 | 104.37 | 5.76 | 55 | 112.22 | 6.73 | 37 |
| | Male | 111.24 | 6.14 | 54 | 110.74 | 7.44 | 19 | 106.25 | 10.23 | 12 | 118.53 | 3.34 | 17 | 118.41 | 6.18 | 17 | 124.64 | 6.36 | 36 |
| Hand W. (width, mm) | Female | 36.38 | 2.00 | 64 | 38.16 | 2.57 | 309 | 37.65 | 2.23 | 26 | 36.88 | 1.25 | 8 | 37.43 | 2.23 | 37 | 39.79 | 3.21 | 39 |
| | Male | 38.89 | 2.54 | 45 | 43.68 | 4.20 | 19 | 43.50 | 3.58 | 12 | 41.29 | 2.11 | 17 | 43.30 | 2.79 | 10 | 44.14 | 2.76 | 35 |
| Thigh L. | Female | 164.65 | 7.09 | 70 | 170.41 | 8.24 | 353 | 161.52 | 7.52 | 25 | 163.91 | 3.62 | 11 | 170.79 | 13.07 | 65 | 180.48 | 8.02 | 40 |
| | Male | 182.46 | 9.22 | 54 | 188.81 | 12.00 | 21 | 185.83 | 12.25 | 12 | 187.20 | 12.33 | 20 | 202.71 | 18.26 | 28 | 203.61 | 10.01 | 36 |
| Leg L. | Female | 151.44 | 6.19 | 70 | 155.59 | 7.92 | 348 | 147.78 | 6.49 | 23 | 146.91 | 5.47 | 11 | 159.98 | 8.89 | 65 | 168.60 | 8.73 | 40 |
| | Male | 168.24 | 7.98 | 54 | 176.62 | 13.20 | 21 | 172.64 | 9.16 | 11 | 168.10 | 9.89 | 20 | 178.46 | 8.98 | 28 | 186.81 | 10.39 | 36 |
| Foot L. | Female | 150.71 | 6.19 | 70 | 154.40 | 6.06 | 324 | 139.23 | 4.16 | 26 | 148.60 | 5.02 | 10 | 154.99 | 6.00 | 56 | 163.73 | 6.63 | 40 |
| | Male | 164.15 | 7.30 | 54 | 169.95 | 8.02 | 21 | 158.83 | 4.00 | 12 | 168.61 | 4.98 | 18 | 174.12 | 7.37 | 17 | 181.20 | 6.39 | 35 |
| Foot W. | Female | 37.23 | 2.00 | 70 | 39.20 | 2.51 | 324 | 37.58 | 2.35 | 26 | 36.90 | 0.88 | 10 | 37.65 | 2.24 | 56 | 39.53 | 2.58 | 40 |
| | Male | 39.94 | 2.10 | 54 | 44.14 | 4.22 | 21 | 44.75 | 2.53 | 12 | 41.58 | 2.01 | 19 | 43.35 | 1.97 | 17 | 44.29 | 2.86 | 35 |
| Head L. | Female | 88.19 | 2.76 | 70 | 93.98 | 3.31 | 325 | 88.92 | 2.68 | 26 | 96.36 | 4.48 | 11 | 98.10 | 3.89 | 56 | 96.73 | 3.70 | 40 |
| | Male | 92.93 | 4.37 | 54 | 99.55 | 4.57 | 20 | 95.08 | 2.97 | 12 | 102.65 | 4.90 | 20 | 105.64 | 4.09 | 14 | 102.75 | 3.43 | 36 |
| Head W. | Female | 71.08 | 2.48 | 70 | 76.05 | 3.19 | 325 | 75.08 | 2.45 | 26 | 76.64 | 2.87 | 11 | 78.67 | 4.13 | 56 | 77.78 | 2.64 | 40 |
| | Male | 75.93 | 4.70 | 54 | 85.70 | 6.79 | 20 | 83.08 | 5.73 | 12 | 83.90 | 4.24 | 20 | 88.71 | 7.22 | 14 | 86.83 | 4.65 | 36 |
| Bizygomatic W. | Female | 82.10 | 2.82 | 70 | 84.73 | 4.19 | 325 | 84.77 | 3.12 | 26 | 84.09 | 3.94 | 11 | 89.73 | 3.87 | 56 | 88.53 | 3.37 | 40 |
| | Male | 90.11 | 5.68 | 54 | 94.00 | 6.16 | 20 | 97.25 | 8.01 | 12 | 95.95 | 6.35 | 20 | 104.64 | 4.36 | 14 | 99.44 | 5.25 | 36 |
| Upper facial H. | Female | 44.08 | 4.04 | 64 | 46.60 | 4.95 | 314 | 57.27 | 7.35 | 26 | 49.80 | 2.90 | 10 | 56.92 | 5.31 | 37 | 49.10 | 4.49 | 40 |
| | Male | 51.26 | 6.40 | 43 | 56.45 | 8.83 | 20 | 71.25 | 9.18 | 12 | 57.89 | 5.72 | 19 | 67.25 | 5.31 | 8 | 55.83 | 6.50 | 35 |
| Head H. | Female | 45.23 | 4.46 | 64 | 46.96 | 5.22 | 312 | 43.35 | 5.21 | 26 | 52.40 | 5.15 | 10 | 46.25 | 5.61 | 28 | 48.43 | 5.19 | 40 |
| | Male | 46.23 | 5.03 | 43 | 46.95 | 4.94 | 20 | 43.36 | 7.32 | 11 | 55.44 | 4.80 | 18 | 53.13 | 4.82 | 8 | 49.46 | 7.77 | 35 |
| Ear L. | Female | 41.30 | 1.88 | 63 | 41.61 | 2.67 | 286 | 40.91 | 3.06 | 23 | 41.80 | 1.69 | 10 | 42.98 | 3.41 | 35 | 43.45 | 2.95 | 33 |
| | Male | 43.81 | 2.51 | 43 | 46.40 | 3.69 | 20 | 45.42 | 2.64 | 12 | 47.84 | 3.56 | 19 | 49.00 | 4.62 | 10 | 48.12 | 4.14 | 33 |
| Ear W. | Female | 28.61 | 1.77 | 63 | 30.01 | 2.40 | 286 | 30.17 | 3.37 | 23 | 30.60 | 1.51 | 10 | 30.69 | 2.69 | 35 | 32.76 | 2.92 | 34 |
| | Male | 30.77 | 3.00 | 43 | 33.20 | 2.31 | 20 | 33.83 | 1.90 | 12 | 34.47 | 3.20 | 19 | 34.50 | 3.24 | 10 | 35.30 | 2.99 | 33 |

SD, standard deviation; *n*, sample size; H, height; L, length; W, width

| Wakasa (Tottori) | | | Takahama (Fukui) | | | Hakushan (Ishikawa) | | | Nikko (Tochigi) | | | Shiga Heights (Nagano) | | | Rhesus (China) | | | Rhesus (India) | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Average | SD | *n* | Average | SD | *n* | Average | SD | *n* | Average | SD | *n* | Average | SD | *n* | Average | SD | *n* | Average | SD | *n* |
| 10.62 | 2.26 | 36 | 8.75 | 1.18 | 66 | 12.77 | 1.27 | 14 | 9.27 | 0.85 | 20 | 11.68 | 1.65 | 47 | 7.77 | 1.37 | 36 | 7.92 | 1.90 | 17 |
| 13.47 | 3.30 | 13 | 13.00 | 1.82 | 55 | | | | 12.09 | 1.09 | 15 | 13.54 | 2.07 | 23 | 12.10 | 1.85 | 15 | 9.80 | 2.51 | 6 |
| 552.92 | 19.50 | 36 | 558.62 | 27.60 | 66 | 564.57 | 14.48 | 14 | 545.35 | 17.04 | 20 | 567.64 | 25.55 | 47 | 525.36 | 22.41 | 36 | 501.15 | 38.94 | 17 |
| 611.19 | 36.86 | 13 | 621.67 | 15.84 | 55 | | | | 590.73 | 26.86 | 15 | 610.89 | 25.16 | 23 | 585.22 | 30.05 | 14 | 545.46 | 55.86 | 6 |
| 377.51 | 16.57 | 36 | 380.10 | 21.35 | 66 | 393.57 | 14.77 | 14 | 366.95 | 15.10 | 20 | 388.70 | 21.24 | 47 | 356.34 | 18.17 | 36 | 342.34 | 28.32 | 16 |
| 414.92 | 27.09 | 13 | 421.21 | 11.47 | 55 | | | | 399.07 | 21.14 | 15 | 408.26 | 20.64 | 23 | 396.20 | 25.65 | 15 | 372.54 | 37.45 | 6 |
| 83.60 | 8.95 | 13 | 86.30 | 11.98 | 39 | 75.21 | 8.75 | 14 | 76.11 | 9.73 | 19 | 79.55 | 8.88 | 42 | 188.61 | 15.82 | 14 | 220.88 | 18.01 | 16 |
| 92.00 | 5.66 | 2 | | | | | | | 84.60 | 14.63 | 15 | 89.52 | 10.12 | 23 | 217.67 | 32.56 | 9 | 249.58 | 9.91 | 6 |
| 452.57 | 38.73 | 34 | 425.16 | 27.95 | 64 | 523.43 | 32.13 | 14 | 451.30 | 34.34 | 20 | 479.57 | 36.42 | 47 | 409.31 | 37.43 | 36 | 411.69 | 43.44 | 13 |
| 476.17 | 48.64 | 12 | 492.80 | 32.52 | 50 | | | | 497.87 | 39.53 | 15 | 494.48 | 26.94 | 23 | 461.00 | 27.37 | 15 | 455.90 | 65.58 | 5 |
| 159.06 | 8.44 | 31 | 156.77 | 6.95 | 62 | 156.43 | 7.62 | 14 | 152.50 | 6.89 | 20 | 156.98 | 7.41 | 43 | 152.39 | 10.06 | 33 | 140.03 | 11.63 | 13 |
| 181.25 | 15.00 | 8 | 179.09 | 4.60 | 34 | | | | 172.00 | 9.03 | 15 | 167.61 | 9.09 | 23 | 173.89 | 14.29 | 15 | 156.87 | 20.09 | 5 |
| 160.47 | 7.88 | 31 | 162.54 | 7.36 | 61 | 162.21 | 5.28 | 14 | 159.40 | 6.30 | 20 | 160.65 | 9.66 | 43 | 156.18 | 8.95 | 33 | 144.55 | 11.32 | 13 |
| 187.00 | 14.89 | 8 | 189.88 | 4.77 | 33 | | | | 178.87 | 9.35 | 15 | 173.00 | 11.25 | 22 | 175.48 | 15.75 | 15 | 162.17 | 23.07 | 5 |
| 106.05 | 3.21 | 21 | 108.00 | 4.77 | 52 | 113.64 | 3.50 | 14 | 101.94 | 3.53 | 16 | 110.38 | 4.52 | 42 | 109.28 | 5.98 | 25 | 101.00 | 4.53 | 12 |
| 120.00 | 4.08 | 4 | 124.94 | 2.92 | 18 | | | | 112.23 | 5.40 | 13 | 119.55 | 7.22 | 22 | 124.15 | 9.29 | 12 | 110.24 | 8.68 | 5 |
| 38.60 | 1.67 | 5 | 36.71 | 1.71 | 24 | 39.00 | 1.92 | 14 | 36.93 | 2.22 | 15 | 40.60 | 1.94 | 42 | 35.15 | 2.29 | 10 | 32.33 | 2.16 | 6 |
| 40.00 | | 1 | 43 | 1.41 | 2 | | | | 41.08 | 1.44 | 13 | 44.18 | 2.44 | 22 | 39.67 | 2.50 | 6 | 34.83 | 4.75 | 3 |
| 178.38 | 12.37 | 31 | 180.49 | 8.27 | 62 | 180.64 | 10.02 | 14 | 172.55 | 7.53 | 20 | 176.51 | 11.04 | 43 | 172.31 | 10.81 | 33 | 165.12 | 14.22 | 13 |
| 212.75 | 18.23 | 8 | 214.00 | 7.38 | 33 | | | | 198.53 | 7.73 | 15 | 189.57 | 16.38 | 23 | 202.77 | 21.04 | 15 | 188.80 | 26.72 | 5 |
| 158.90 | 9.64 | 31 | 163.21 | 7.57 | 61 | 166.79 | 9.58 | 14 | 160.26 | 8.64 | 19 | 164.16 | 10.04 | 43 | 155.13 | 7.33 | 33 | 151.56 | 12.52 | 13 |
| 181.38 | 14.33 | 8 | 189.91 | 6.73 | 33 | | | | 179.38 | 8.18 | 13 | 180.86 | 13.21 | 22 | 182.45 | 16.56 | 15 | 167.13 | 19.48 | 5 |
| 156.17 | 5.03 | 22 | 159.40 | 5.48 | 54 | 166.36 | 4.18 | 14 | 148.90 | 4.48 | 20 | 164.26 | 6.25 | 42 | 159.88 | 7.95 | 24 | 147.10 | 8.88 | 13 |
| 177.50 | 13.70 | 4 | 180.11 | 2.59 | 18 | | | | 166.87 | 8.11 | 15 | 179.00 | 7.86 | 23 | 177.70 | 11.54 | 10 | 161.67 | 12.24 | 5 |
| 38.41 | 1.48 | 22 | 37.60 | 1.86 | 54 | 41.14 | 2.21 | 14 | 37.43 | 1.60 | 14 | 41.19 | 1.57 | 42 | 36.04 | 1.98 | 24 | 33.10 | 2.09 | 13 |
| 43.75 | 1.26 | 4 | 42.72 | 1.13 | 18 | | | | 41.67 | 1.99 | 15 | 45.96 | 3.11 | 23 | 40.25 | 2.37 | 10 | 35.67 | 3.70 | 5 |
| 98.46 | 4.86 | 20 | 99.54 | 3.37 | 51 | 98.21 | 2.33 | 14 | 92.79 | 2.59 | 19 | 99.33 | 3.18 | 43 | 92.76 | 4.73 | 23 | 91.13 | 5.30 | 13 |
| 105.25 | 6.75 | 4 | 107.88 | 3.31 | 17 | | | | 98.40 | 3.40 | 15 | 103.52 | 3.45 | 23 | 102.18 | 4.58 | 11 | 100.73 | 8.21 | 5 |
| 81.98 | 4.38 | 20 | 80.48 | 3.70 | 51 | 77.43 | 4.01 | 14 | 76.63 | 2.56 | 19 | 78.23 | 3.32 | 43 | 78.72 | 3.96 | 23 | 75.29 | 3.82 | 13 |
| 94.00 | 9.56 | 4 | 91.75 | 5.17 | 16 | | | | 81.53 | 3.76 | 15 | 83.78 | 2.59 | 23 | 86.68 | 3.59 | 11 | 86.00 | 7.71 | 5 |
| 90.75 | 4.36 | 20 | 91.65 | 2.89 | 51 | 92.36 | 4.03 | 14 | 88.53 | 2.95 | 19 | 91.98 | 3.20 | 43 | 84.24 | 3.82 | 23 | 82.86 | 5.16 | 13 |
| 102.50 | 8.35 | 4 | 108.13 | 1.82 | 16 | | | | 98.40 | 4.90 | 15 | 100.91 | 5.05 | 23 | 96.64 | 4.32 | 11 | 96.80 | 10.47 | 5 |
| 45.80 | 10.28 | 5 | 50.71 | 3.64 | 7 | 53.79 | 4.14 | 14 | 49.85 | 3.22 | 20 | 53.86 | 3.42 | 43 | 39.50 | 5.42 | 8 | 39.80 | 5.02 | 5 |
| 59.00 | | 1 | | | | | | | 59.20 | 4.72 | 15 | 62.24 | 6.54 | 21 | 52.50 | 5.09 | 6 | 46.67 | 5.13 | 3 |
| 49.00 | 7.07 | 4 | 49.57 | 5.47 | 7 | 43.64 | 2.17 | 14 | 50.35 | 6.12 | 20 | 47.29 | 5.96 | 42 | 39.88 | 4.64 | 8 | 44.00 | 6.60 | 5 |
| 40.00 | | 1 | | | | | | | 54.80 | 5.51 | 15 | 46.22 | 5.17 | 18 | 39.75 | 3.60 | 6 | 36.83 | 1.26 | 3 |
| 44.60 | 2.97 | 5 | 42.94 | 2.49 | 16 | 43.36 | 2.47 | 14 | 42.13 | 1.92 | 15 | 46.95 | 2.49 | 40 | 41.21 | 4.16 | 7 | 39.00 | 0.82 | 4 |
| 51.00 | | 1 | | | | | | | 46.45 | 2.81 | 11 | 49.35 | 3.11 | 23 | 46.10 | 2.92 | 5 | 43.50 | 0.71 | 2 |
| 31.80 | 2.68 | 5 | 31.69 | 1.96 | 16 | 34.50 | 3.30 | 14 | 29.73 | 2.15 | 15 | 33.63 | 2.50 | 41 | 30.21 | 4.30 | 7 | 27.75 | 5.74 | 4 |
| 37.00 | | 1 | | | | | | | 32.27 | 2.00 | 11 | 35.32 | 2.42 | 22 | 34.40 | 2.70 | 5 | 33.50 | 3.54 | 2 |

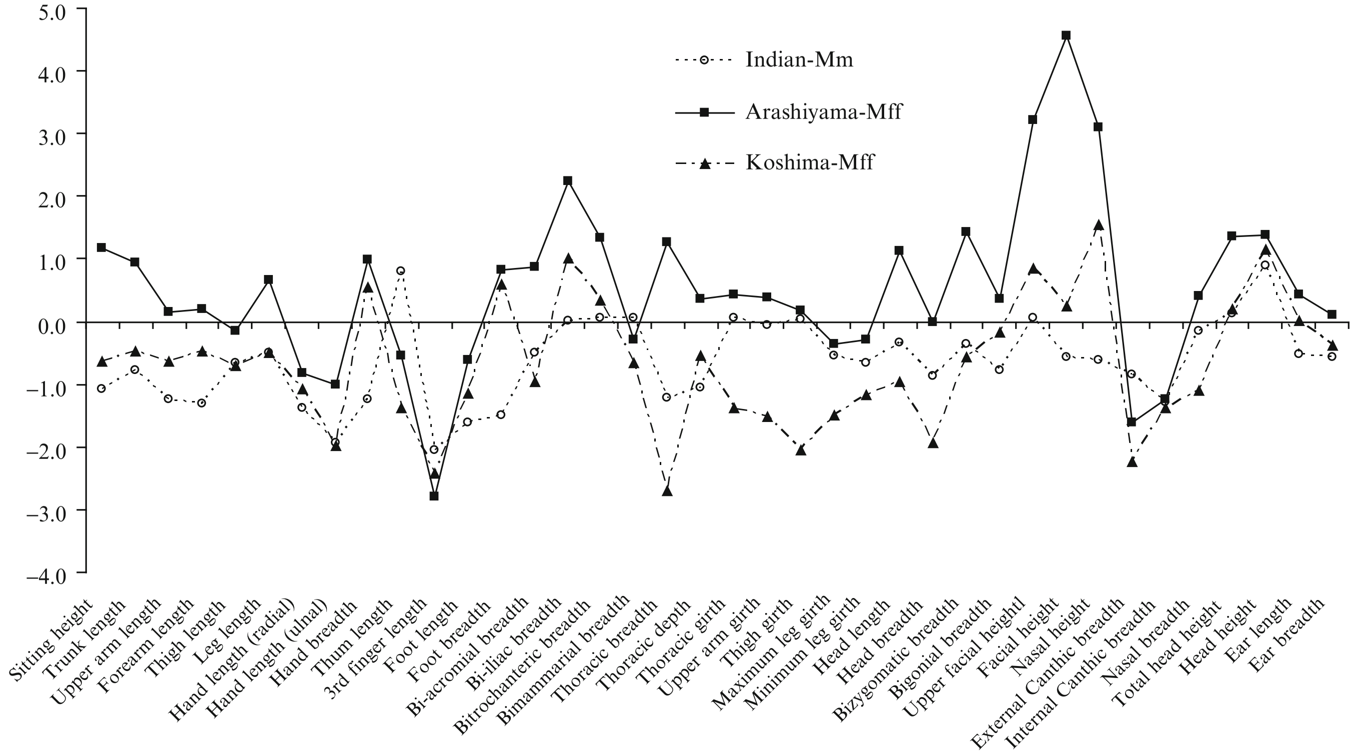

**Fig. 2.5** Deviation diagram of the somatometric characteristics in Arashiyama and Koshima Japanese macaques. (From Hamada 2008.) The deviation was calculated from the average and standard deviation of Chinese rhesus macaques. For comparison, the deviation graph of Indian rhesus macaques (*dotted line*) is superimposed

Deciduous dentition is almost completed within the infantile period (Iwamoto et al. 1984), when the individual can take food independently without being fed by the mother. However, juveniles follow their mothers in ranging and depend on their mother's knowledge about when and where foods are found (for details, see Chap. 11).

At about 3–4 months of age, the neonatal coat hair changes to hair of the same color as that of an adult. At the end of the infantile period, locomotor function has developed so the individual can forage by itself without being carried by its mother. Because of this rapid development in independent feeding and locomotion, the mother's period of intense duty is shortened (Hamada 1999). In this respect, Japanese macaques are considered to have adopted an energy strategy in infantile development, which enables the mother to give birth every year in cases in which the mother can restore her energy after weaning, although the average interbirth interval is longer than 1 year (see Chap. 11). The rapid infantile growth increases the number of offspring in the female Japanese macaque's life. This is the reproductive strategy cercopithecoids have adopted, which is represented by savanna-dwelling cercopithecids such as *Cercopithecus aethiops* (whose interbirth interval is 365 days; Harvey et al. 1987) and *Erythrocebus patas* (whose interbirth interval is ca. 440 days; Nakagawa et al. 2003). On the other hand, younger juveniles must often live without being fed by the mother in winter, a food-scarce season, and thus, the mortality of younger juveniles is high (Taroda-Takizawa 2002). This high rate may be compensated by births earlier in the year in Japanese macaque populations inhabiting higher latitudes than those inhabiting lower latitudes (Fooden and Aimi 2003).

### *2.3.2 Juvenile Period*

The juvenile period is demarcated by both onset of weaning and reproductive maturation, spanning 0.5–3.5 years in females and 0.5–4.5 years in males, on average (but see Chap. 11). There is considerable interindividual variability in the age of reproductive maturation, and early and late maturers are found. In the juvenile period, development of special function(s) is not found, which is different from the infantile and adolescent periods. The duration of the juvenile period, 3 and 4 years in females and in males, respectively, is rather long. The juvenile period is supposed to be the period in which to learn (accumulate information and experience about) the social way of life (Hamada 2007).

Striking seasonal fluctuation is found in body weight increase (Fig. 2.6a). In the growth of linear dimension (anterior trunk length), factoring out the trend (average growth) from the growth curve reveals a circannual fluctuation of about 2 mm amplitude, with the peak in late fall to winter.

Juvenile and older individuals of Japanese macaques molt once a year in early summer. Because the distal tip of the hair is darkish, the individuals with shorter (growing) hairs appear blackish in the period from summer to early fall

**Table 2.2** Body proportions (%) in Japanese and rhesus macaques (Hamada 2008)

| | | Locality (Prefecture) | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Koshima (Miyazaki) | | | Takasakiyama (Oita) | | | Shodoshima (Kagawa) | | | Awajishima (Hyogo) | | | Arashiyama (Kyoto) | | | Hagachizaki (Shizuoka) | | |
| Proportions | Sex | Average | SD | *n* | Average | SD | *n* | Average | SD | *n* | Average | SD | *n* | Average | SD | *n* | Average | SD | *n* |
| Relative tail L. | Female | 13.74 | 2.40 | 85 | 16.18 | 2.20 | 300 | 16.94 | 1.88 | 26 | 15.37 | 0.67 | 10 | 14.44 | 1.89 | 42 | 13.05 | 2.25 | 36 |
| | Male | 14.00 | 2.72 | 58 | 16.57 | 2.90 | 20 | 17.42 | 1.71 | 11 | 15.74 | 1.50 | 19 | 14.41 | 2.05 | 14 | 13.56 | 2.14 | 34 |
| Brachial I. | Female | 103.98 | 2.09 | 70 | 105.12 | 4.25 | 326 | 103.79 | 10.34 | 26 | 105.17 | 4.20 | 11 | 102.70 | 4.50 | 65 | 106.89 | 4.68 | 40 |
| | Male | 104.95 | 3.65 | 53 | 102.95 | 6.53 | 21 | 104.48 | 7.71 | 12 | 104.73 | 4.09 | 19 | 102.86 | 5.46 | 27 | 106.98 | 6.40 | 36 |
| Crural I. | Female | 92.02 | 2.35 | 70 | 91.35 | 3.89 | 348 | 91.45 | 5.24 | 23 | 89.62 | 2.46 | 11 | 94.17 | 8.38 | 65 | 93.46 | 3.85 | 40 |
| | Male | 92.25 | 2.55 | 54 | 93.61 | 5.04 | 21 | 93.81 | 5.61 | 11 | 89.92 | 3.76 | 20 | 88.76 | 9.53 | 28 | 91.86 | 5.23 | 36 |
| Intermembranal I. | Female | 94.27 | 1.74 | 70 | 92.97 | 2.97 | 322 | 96.17 | 5.48 | 23 | 94.30 | 3.11 | 11 | 94.41 | 3.21 | 65 | 91.97 | 2.98 | 40 |
| | Male | 93.03 | 6.45 | 54 | 92.77 | 4.05 | 21 | 101.88 | 24.62 | 12 | 89.69 | 9.92 | 20 | 90.64 | 17.89 | 28 | 91.30 | 3.09 | 36 |
| Head L./Head W. | Female | 80.64 | 2.51 | 70 | 80.98 | 3.50 | 325 | 84.48 | 3.29 | 26 | 79.62 | 3.51 | 11 | 80.22 | 3.41 | 56 | 80.47 | 2.84 | 40 |
| | Male | 81.75 | 4.29 | 54 | 86.10 | 5.76 | 20 | 87.44 | 6.31 | 12 | 81.82 | 4.25 | 20 | 83.92 | 5.03 | 14 | 84.55 | 4.42 | 36 |
| Upper facial H./ Bizomatic W. | Female | 53.80 | 4.58 | 64 | 54.94 | 4.98 | 313 | 67.54 | 8.19 | 26 | 58.56 | 3.80 | 10 | 64.07 | 6.06 | 37 | 55.48 | 4.84 | 40 |
| | Male | 57.57 | 6.49 | 43 | 59.82 | 6.59 | 20 | 73.36 | 7.84 | 12 | 59.84 | 5.06 | 19 | 65.78 | 4.81 | 8 | 56.10 | 5.68 | 35 |
| Upper facial H./ Head L. | Female | 49.96 | 4.26 | 64 | 49.57 | 5.07 | 313 | 64.45 | 8.47 | 26 | 51.56 | 4.75 | 10 | 58.79 | 5.72 | 37 | 50.77 | 4.26 | 40 |
| | Male | 55.34 | 6.77 | 43 | 56.54 | 7.23 | 20 | 74.88 | 8.78 | 12 | 56.02 | 5.55 | 19 | 64.71 | 5.16 | 8 | 54.24 | 6.01 | 35 |
| Hand L./Arm L. | Female | 34.54 | 1.25 | 70 | 34.25 | 1.73 | 321 | 29.99 | 2.07 | 25 | 35.41 | 1.32 | 9 | 33.55 | 1.50 | 55 | 34.98 | 1.69 | 37 |
| | Male | 34.42 | 4.73 | 54 | 32.51 | 2.51 | 19 | 31.28 | 3.25 | 12 | 36.00 | 1.03 | 17 | 33.84 | 1.27 | 17 | 35.02 | 1.76 | 36 |
| Foot L./Foot W. | Female | 24.72 | 1.21 | 70 | 25.40 | 1.47 | 324 | 27.01 | 1.92 | 26 | 24.85 | 0.94 | 10 | 24.31 | 1.41 | 56 | 24.14 | 1.13 | 40 |
| | Male | 24.34 | 0.92 | 54 | 25.95 | 1.79 | 21 | 28.18 | 1.60 | 12 | 24.83 | 1.17 | 18 | 24.93 | 1.39 | 17 | 24.45 | 1.53 | 35 |
| Foot L./(thigh and leg)L. | Female | 47.71 | 1.51 | 70 | 47.80 | 5.39 | 323 | 48.51 | 12.12 | 25 | 47.64 | 1.70 | 10 | 46.96 | 1.88 | 56 | 46.95 | 1.99 | 40 |
| | Male | 46.84 | 1.63 | 54 | 46.58 | 1.65 | 21 | 47.57 | 11.07 | 12 | 46.94 | 1.44 | 18 | 46.74 | 2.12 | 17 | 46.48 | 2.03 | 35 |
| Hand L./Foot L. | Female | 68.26 | 1.53 | 70 | 67.36 | 2.96 | 319 | 63.88 | 5.31 | 25 | 69.57 | 1.46 | 9 | 67.32 | 2.34 | 55 | 68.62 | 3.00 | 37 |
| | Male | 67.78 | 2.42 | 54 | 64.89 | 4.48 | 19 | 66.83 | 5.42 | 12 | 70.27 | 1.25 | 17 | 68.02 | 2.55 | 17 | 68.93 | 3.69 | 35 |

SD, standard deviation; *n*, sample size

("summer-hair"), and those with longer but tip-worn hair appear whitish in the period from winter to spring ("winter-hair"; Hamada, personal observation).

### 2.3.3 Adolescent Period

The adolescent period starts around the time of reproductive maturation, that is, at menarche (and first swelling and reddening of sexual skin – exposed skin around anus, genitalia, and posterior aspect of thigh) in females and the rapid growth of testes in males, and it ends when growth becomes very slow and the permanent dentition completes. Together with reproductive maturation, secondary sexual

| Wakasa (Tottori) | | | Takahama (Fukui) | | | Hakusan (Ishikawa) | | | Nikko (Tochigi) | | | Shiga Heights (Nagano) | | | Rhesus (China) | | | Rhesus (India) | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Average | SD | *n* | Average | SD | *n* | Average | SD | *n* | Average | SD | *n* | Average | SD | *n* | Average | SD | *n* | Average | SD | *n* |
| 15.28 | 1.66 | 13 | 15.43 | 2.14 | 39 | 13.32 | 1.50 | 14 | 13.93 | 1.61 | 19 | 14.02 | 1.71 | 42 | 36.52 | 2.85 | 14 | 44.19 | 4.91 | 16 |
| 14.36 | 0.43 | 2 | | | | | | | 14.33 | 2.40 | 15 | 14.66 | 1.55 | 23 | 37.80 | 4.31 | 9 | 46.08 | 4.06 | 6 |
| 101.00 | 3.64 | 31 | 103.74 | 3.91 | 61 | 103.79 | 2.49 | 14 | 104.65 | 4.85 | 20 | 102.49 | 6.63 | 43 | 102.58 | 3.24 | 33 | 103.30 | 2.88 | 13 |
| 103.22 | 2.18 | 8 | 106.10 | 4.00 | 33 | | | | 104.10 | 4.86 | 15 | 103.60 | 8.02 | 22 | 100.88 | 2.48 | 15 | 103.25 | 2.53 | 5 |
| 89.45 | 5.72 | 31 | 90.52 | 3.65 | 61 | 92.54 | 6.90 | 14 | 92.69 | 2.65 | 19 | 93.18 | 5.57 | 43 | 90.17 | 3.36 | 33 | 91.89 | 4.33 | 13 |
| 85.31 | 1.97 | 8 | 88.84 | 4.25 | 33 | | | | 91.21 | 3.23 | 13 | 96.04 | 6.83 | 22 | 90.17 | 3.72 | 15 | 88.83 | 3.46 | 5 |
| 95.00 | 3.11 | 31 | 92.16 | 6.54 | 61 | 91.77 | 2.72 | 14 | 93.76 | 3.40 | 19 | 93.38 | 4.37 | 43 | 94.26 | 3.21 | 33 | 89.91 | 2.36 | 13 |
| 93.48 | 2.47 | 8 | 91.39 | 2.00 | 33 | | | | 103.66 | 29.68 | 15 | 92.01 | 5.26 | 23 | 90.82 | 2.95 | 15 | 89.57 | 0.78 | 5 |
| 83.31 | 2.92 | 20 | 80.90 | 3.72 | 51 | 78.88 | 4.55 | 14 | 82.63 | 3.20 | 19 | 78.83 | 3.99 | 43 | 85.00 | 4.98 | 23 | 82.68 | 1.90 | 13 |
| 89.18 | 4.06 | 4 | 85.12 | 5.37 | 16 | | | | 82.92 | 4.13 | 15 | 80.99 | 2.97 | 23 | 84.89 | 2.97 | 11 | 85.42 | 4.76 | 5 |
| 51.48 | 8.91 | 5 | 56.33 | 3.49 | 7 | 58.31 | 4.96 | 14 | 56.12 | 2.94 | 19 | 58.56 | 3.21 | 43 | 47.64 | 4.76 | 8 | 50.47 | 3.68 | 5 |
| 58.42 | | 1 | | | | | | | 60.12 | 2.83 | 15 | 61.70 | 5.57 | 21 | 55.71 | 5.01 | 6 | 50.69 | 3.21 | 3 |
| 48.91 | 11.88 | 5 | 51.39 | 3.95 | 7 | 54.76 | 3.92 | 14 | 53.55 | 3.21 | 19 | 54.26 | 3.58 | 43 | 43.77 | 5.00 | 8 | 45.27 | 3.83 | 5 |
| 55.14 | | 1 | | | | | | | 60.11 | 3.46 | 15 | 60.27 | 6.94 | 21 | 51.96 | 5.04 | 6 | 48.58 | 4.01 | 3 |
| 33.63 | 1.49 | 21 | 33.77 | 1.28 | 51 | 35.72 | 1.84 | 14 | 32.75 | 1.05 | 16 | 34.75 | 1.86 | 42 | 35.48 | 1.87 | 25 | 35.25 | 2.20 | 12 |
| 33.93 | 1.77 | 4 | 34.01 | 0.86 | 18 | | | | 32.05 | 1.06 | 13 | 36.74 | 7.38 | 22 | 34.28 | 2.49 | 12 | 32.64 | 3.01 | 5 |
| 24.61 | 1.02 | 22 | 23.67 | 1.33 | 54 | 24.73 | 1.18 | 14 | 25.08 | 1.10 | 14 | 25.10 | 1.18 | 42 | 22.56 | 0.95 | 24 | 22.54 | 1.30 | 13 |
| 24.72 | 1.26 | 4 | 23.73 | 0.80 | 18 | | | | 25.00 | 1.19 | 15 | 25.70 | 1.76 | 23 | 22.70 | 1.44 | 10 | 22.04 | 1.11 | 5 |
| 46.26 | 1.74 | 22 | 47.10 | 6.17 | 54 | 47.94 | 1.57 | 14 | 46.93 | 9.62 | 20 | 48.20 | 2.48 | 42 | 48.96 | 2.02 | 24 | 46.56 | 2.11 | 13 |
| 47.15 | 1.41 | 4 | 44.59 | 1.36 | 18 | | | | 49.22 | 13.65 | 15 | 50.27 | 8.54 | 23 | 47.30 | 2.07 | 10 | 45.71 | 2.98 | 5 |
| 68.27 | 2.02 | 21 | 67.63 | 2.29 | 51 | 68.33 | 2.03 | 14 | 68.75 | 1.99 | 16 | 67.26 | 2.99 | 42 | 68.25 | 2.35 | 24 | 68.56 | 2.53 | 12 |
| 67.77 | 2.92 | 4 | 69.37 | 1.16 | 18 | | | | 67.60 | 2.46 | 13 | 66.90 | 3.36 | 22 | 69.34 | 2.48 | 10 | 68.22 | 2.53 | 5 |

characteristics develop in this period, such as teat growth, and the sexual skin swells with the menstrual cycle and reddens. Facial skin also reddens. In males, the musculoskeletal system develops, and the facial skin, scrotum, and posterior aspect of the thigh redden in the mating season (Nigi et al. 1980).

Some females ovulate at 3.5 years and become pregnant in the first mating season to give birth at about 4 years of age; however, the majority of females give birth the next year (fifth year of life; see Chap. 11). The determining factor of reproductive maturation in females is physical development, which could be represented by body weight; 6 kg is a rough estimate (threshold) for females to attain reproductive maturation (Hamada et al. 1999). Although adolescent females remain in their natal group, their male counterparts leave to forage by themselves or with a male group independently from the social group (Sprague et al. 1998).

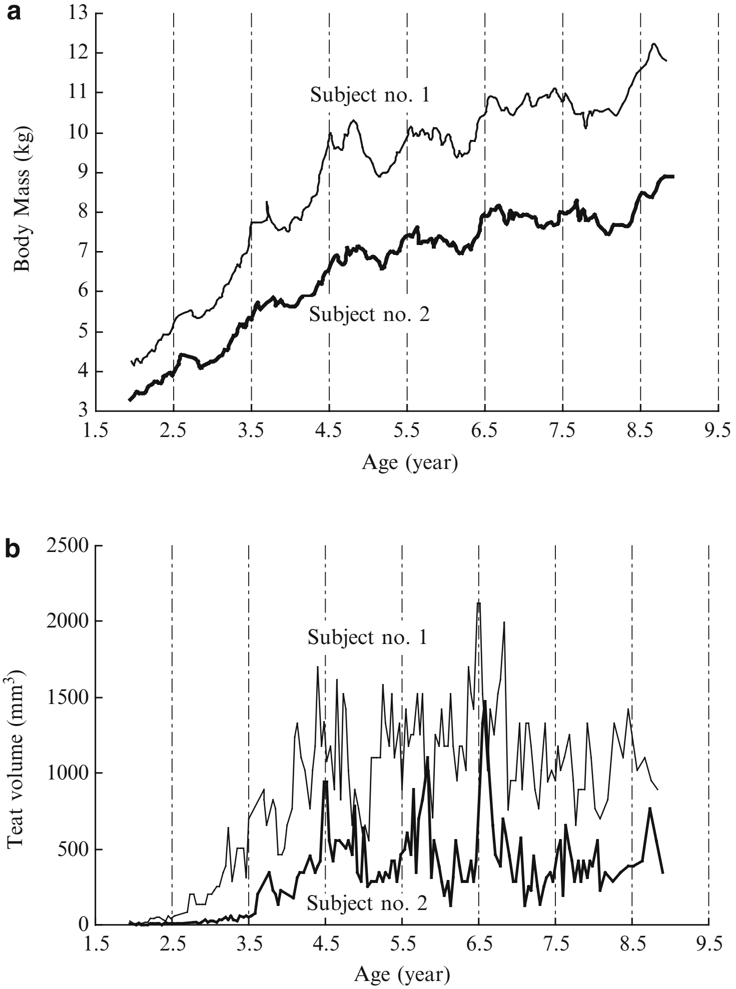

**Fig. 2.6** Increase in body weight (**a**) and teat volume (**b**) in two female Japanese macaques from juvenile to subadult stages. (From Hamada 2008)

Growth and development in adolescence are rapid in Japanese macaques, and there is wide variation in growth between individuals. Therefore, a longitudinal study is indispensable to describe and analyze Japanese macaque growth and development. Examples of the growth in two captive females are shown in Fig. 2.6a (for body weight); one is for a precocial and the other is for an ordinary growing individual. The growth curves of teat size (in cubic millimeters), which is a good indicator of menstrual cycle and pregnancy, for the same individuals are shown in Fig. 2.6b. Not only the size but also the age at the onset of rapid growth differ between the two individuals (Hamada et al. 2005a). Individual no. 2 grew normally in body and individual no. 1 grew better than average. However, individual no. 1

showed precocial growth in teat size, in which rapid growth started at about 2.5 years and was accelerated at about 3.5 years. After this great increase, the teats became smaller and then again rapidly increased at around 4.5 years. After 4.5 years of age, teat size was stabilized. The time at which teat size increased coincided with the mating season, late fall and winter. On the other hand, the teats of individual no. 2 started to very slowly increase at around 2 years and showed a smaller peak at 3.8 years; a substantial increase to arrive at the annual peak was experienced at around 4.5 years. After 4.5 years of age, the teats appeared to be stabilized in size with circannual fluctuation.

Reproductive maturation in males was traced by the increase of testis size (Fig. 2.7a). In individual no. 3, testis growth was normal, that is, the volume started

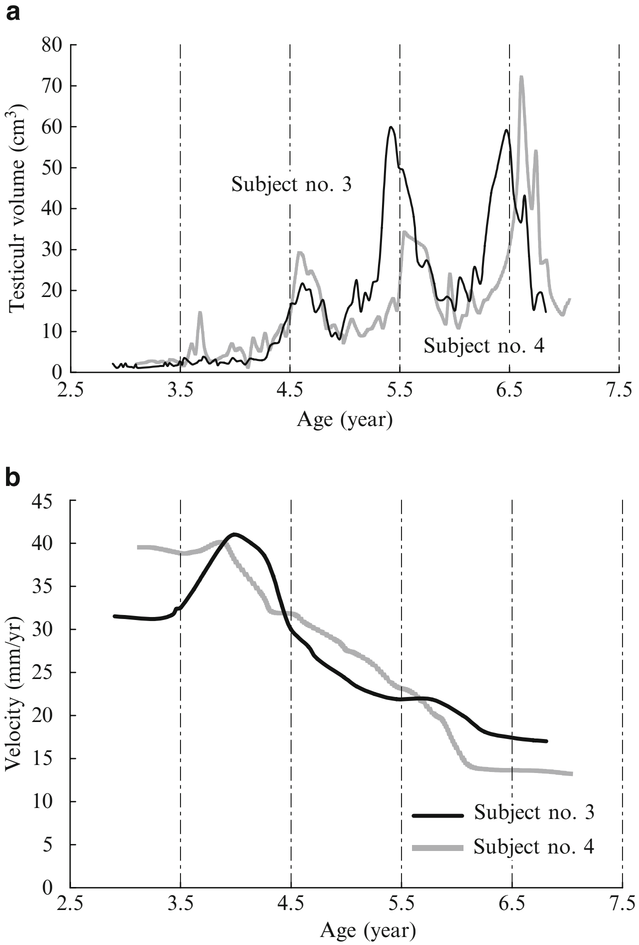

**Fig. 2.7** Growth of testicular volume (**a**) and growth velocity curve of trunk length (**b**) in two male Japanese macaques from juvenile to subadult stages. (From Hamada 2008)

to slowly increase at 4.0 years, increased rapidly at about 4.3 years, and attained its annual peak at 4.7 years. After the peak, testis volume decreased until 5.0 years. From the sixth year of life onward, as shown by the peaks at 5.5 and 6.5 years, the testes appeared to be matured at 5.5 years. Individual no. 4 was precocial as shown by the earlier onset of testis size increase; however, peak testis size was attained at 6.5 years, that is, in mating season, meaning this individual matured reproductively at 6.5 years.

Velocity curves of trunk length for the two male individuals are shown in Fig. 2.7b. Individual no. 3 showed an acceleration phase that attained its peak at about 4.0 years of age. On the other hand, no. 4, the precocial individual, maintained greater velocity, 40 mm/year, until about 4.0 years, after which the velocity decreased. Thus, male Japanese macaques show either acceleration or maintenance of greater velocity of increase during 3.5–5.5 years of age in both body size growth and reproductive development. This growth pattern in later juvenile and adolescent periods appears to be similar to that in humans (Bogin 1999).

It is noteworthy that there is an age discrepancy between physical maturation and reproductive maturation, which is common to Japanese macaques and humans; this means they mature reproductively before the rest of the body has attained maturation (stops increasing in size). Japanese macaque reproductive maturity is at 3.5 or 4.5 years in females and about 5.5 years in males; however, the other body systems keep growing. What adaptational meaning is there in this discrepancy?

It has been hypothesized that the period during which the individual matures reproductively, but not in its whole body system, is a time for learning the ways of social behavior (interaction) with the same or the other sex (Bogin 1999). The ability to acquire food among individuals negotiating with ecological factors is a great influence on growth and maturation. An individual primate living in a society has a social status (rank) that determines the quality and quantity of food it acquires and also its reproductive success (Sugiyama and Ohsawa 1982). Physical maturation thus occurs after acquiring social skills.

Within Japanese macaques, individuals of the Koshima group revealed striking delayed growth and reproductive maturation, which was reflected in testicular growth. On average, these individuals attained adult level as late as 12 years, 5–7 years later than the age of testicular development in caged individuals in PRI, Kyoto University (Fig. 2.8). Females in the Koshima group also showed retardation of reproductive maturation, and some female individuals never produced offspring in their lives (Mori 1979). Japanese macaque individuals show a reaction norm (Stearns 1992), that is, the ability to modify their life history to optimize their growth and maturation pattern to increase their reproductive success according to nutrition (food acquisition). However, the exact nature of the reaction norm in Japanese macaques is the subject of future study.

Fat accumulation is considered to be the determinant factor of the onset of reproductive maturation in females, and it is therefore regarded as a good indicator of nutritional condition, which determines the reproductive outcome in female adults. Although some indices of body fat have been devised, it is difficult to evaluate

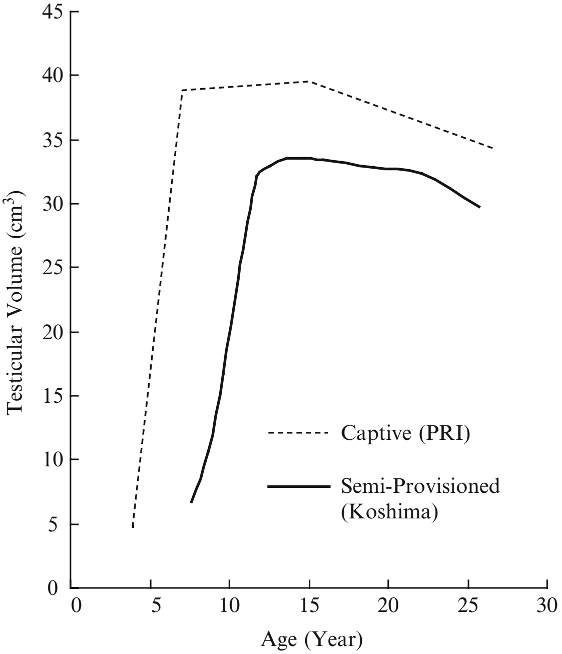

**Fig. 2.8** Age change of testicular volume in captive [Primate Research Institute (PRI), Kyoto University] and free-ranging Japanese macaques (Koshima group). (Data from Hamada et al. 1996a,b)

whole-body fat mass. Dual-energy X-ray absorptiometry (DXA), which was developed for the evaluation of osteoporosis by the measurement of bone density or bone mass, could be used to accurately measure whole-body fat mass. Using DXA, we have examined the age change of fat mass in Japanese macaques. We also analyzed the relationship between fat mass indices calculated from somatometric data [e.g., body mass and trunk length and/or skinfold thickness (SF); Hamada et al. 2003] and fat mass ratio.

Physique index (PI) calculated for Japanese macaques is obtained by the following formula: 1.05 × body weight (kg)/[anterior trunk length (mm)]$^{2.3}$ × $10^7$ for females and body weight (kg)/[anterior trunk length (mm)]$^{2.3}$ × $10^7$ for males (Hamada et al. 2003). The average PI is 100 in both females and males. Another index of body fat is SF, which we measured at the belly (abdominal, beside the umbilicus), back (subscapular, below the inferior angle of the scapula), and side of the belly (just above the suprailiac crest). The summed SF was used for analysis.

Regression and correlation were calculated between the body fat ratios for both sexes (FR, fat mass ratio against body mass) and PIs or SF; $FR = 0.322 \times PI - 26.57$ ($r^2 = 0.759$) and $FR = 0.657 \times SF - 2.306$ ($r^2 = 0.632$). As shown in the highly significant correlation between the PIs and fat mass ratios, PI can be used to estimate fat mass.

An age-change graph was produced for the FR, which was calculated from PIs for caged (reared at the PRI) and Koshima groups (Fig. 2.9a). The two groups showed similar lower FR until 4 years of age. Then, in the caged group, FR increased to about 12% in adults, 10–20 years of age; in comparison, in the Koshima group FR remained as low as 5%. The poor nutritional condition is reflected by the delayed growth and development and lower reproductive output in the Koshima group.

A longitudinal study on the FR and SF was carried out on caged female Japanese macaques (Fig. 2.10). In these subjects, FR remained about 4%, which is

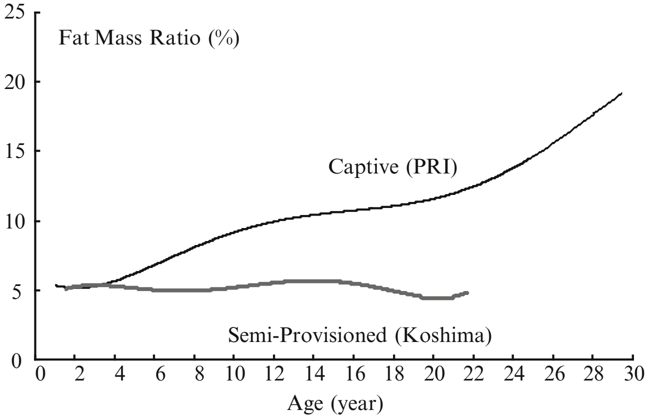

**Fig. 2.9** Age change of fat mass ratio (compared with body mass, %) in captive (PRI, Kyoto University, *thin line*) and free-ranging Japanese macaques (Koshima, *thick line*). (Modified from Fig. 1.6 in Hamada 2008)

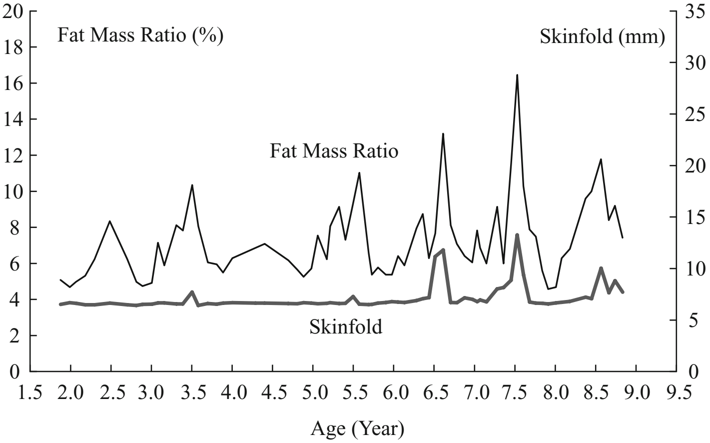

**Fig. 2.10** Age changes of fat mass ratio (against body mass, %) and skinfold thickness (summed thickness at abdominal, back, and suprailiac sites) in artificially reared female Japanese macaques in juvenile and adolescent stages. (From Hamada 2008)

the minimum value of DXA, with small circannual fluctuation from 2 to 6.5 years of age. The energy obtained was not used for fat accumulation but for growth, maintenance, and activities. During the mating season in the seventh year of life (6.5 years of age), FR showed a significant increase, although it again rapidly decreased until 7.0 years of age. Similar fluctuation was repeated in the eighth year of life (7.5–8.0 years of age). Thus, the fat accumulation showed seasonality with a peak in late autumn (the mating season). SF also showed peaks in winter from the age of 2 years onward, and the peaks at 6.5 and 7.5 years of age were significant. Female Japanese macaques start to accumulate fat in late autumn from the age of 6.5 years. The same is true in males, although the magnitude of accumulation is much lower than that in females.

In summary, the reproductive function including the ability to acquire energy (fat accumulation) fully matures at around 7 years of age in Japanese macaques, which time demarcates the end of adolescence. After that age, the subadult stage starts.

### *2.3.4 Subadult and Adult Stages*

In general, the adult stage is considered to start at the age when body growth stops, represented by such whole-body dimensions as stature (or its proxy, trunk length in nonhuman primates). The age at which body growth stops has not been determined for Japanese macaques because body weight fluctuates within a given individual and there is wide variation among individuals after adolescence. Also, the growth in linear dimension is too slow to determine the age of growth cessation. For these reasons, 7 years of age (at which the permanent dentition is fully erupted; Iwamoto et al. 1987) has been regarded as the age demarcating the adult stage, although the actual growth is not known.

In our longitudinal study on Japanese macaques, details of the growth of body weight and trunk length have been described. Body weight and trunk length do increase after 7 years of age until about 15 years of age (Hamada et al., in preparation; Kurita, 2007) However, it is difficult to determine the exact age of growth cessation that is common to individuals because body weight and trunk length showed greater interindividual variation. On the other hand, increase in the length of long bones such as the thigh (femur) can be used to determine the age at growth cessation, as this parameter does not vary greatly with individuals. The thigh length increases until about 10 years of age, after which it showed no significant change (neither increase nor decrease). Thus, 10 years of age is considered as the end of the subadult stage and the start of the adult stage. The increase of trunk length is be described in the next section.

Great interindividual variation was found in the fat accumulation in adults; FR varied from 4% in many individuals to 10–40% in others. From the interlocality comparison in caged Japanese macaques, the frequency of obese individuals (fat accumulation of greater than 20% of body mass) was higher in the Wakasa group

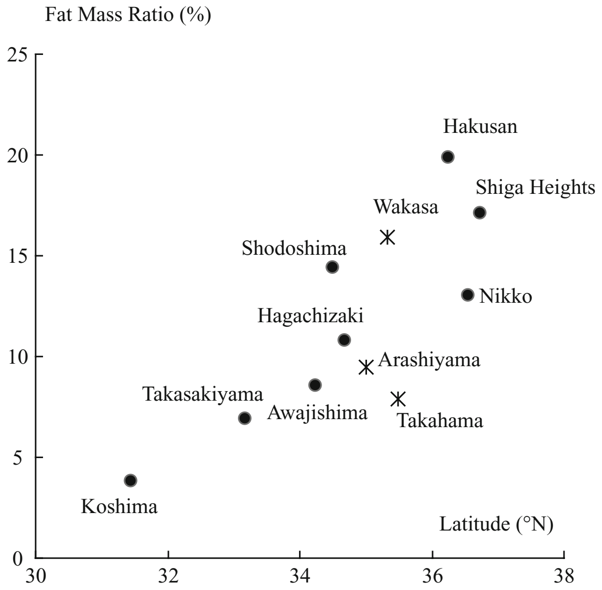

**Fig. 2.11** Geographical variation in fat mass ratio. *Asterisks* show captive populations; *filled circles* show free-ranging populations

(from Tottori Prefecture) than the Arashiyama and Takahama groups (Fukui Prefecture; Takahashi et al. 2005) (Fig. 2.11), which means that they have different genetic and physiological backgrounds of fat accumulation.

The average FR that was estimated from PIs for local groups correlates with habitat latitude (Fig. 2.11). The unprovisioned Hakusan group, which inhabits a locality of cold and heavy snowfalls, has the greatest FR (Hamada et al. 2003), and the Koshima group has the smallest FR. Circannual body weight fluctuation was considerably higher in free-ranging Japanese macaques, by several kilograms (Hazama 1964), suggesting that fat accumulation is vital for the success of reproduction in free-ranging macaques, especially for females (Hamada 2002).

### *2.3.5 Elderly Stage: Morphological Change and Reproductive Activity*

The elderly stage and aging have not been discussed in mammals, except in experimental animals, because the majority of individuals exhibit reproductive activity throughout their lives and they may die before they show physical aging. In this respect, humans are exceptional in that they have significantly long postmenopausal lives and show aging in various organs (Hamada 2004). Thus, the question is whether nonhuman anthropoids have a significant elderly stage and whether Japanese macaques in particular have an elderly age stage and show aging.

In humans, body weight and stature decrease with age as the quantitative signs of physical aging change (Medina 1996; Arking 1998). We examined the age change in body weight and trunk length in adult Japanese macaques. Although reproductive activities (parity and lactation) influence the aging processes, they are not considered here because of the paucity of data. Here we show data on aging in the PRI (caged and provisioned) and Koshima (free-ranging and temporarily provisioned) subjects. Female subjects used here had given birth and taken care of their offspring at least until the second year of life. Figure 2.12 shows the age-change graphs in both the PRI and Koshima groups. We considered 99% of maximum body size in the age-change curve to demarcate the adult (prime) stage. We obtained the ages at first attaining and first becoming smaller than 99% of maximum (Hamada et al., in

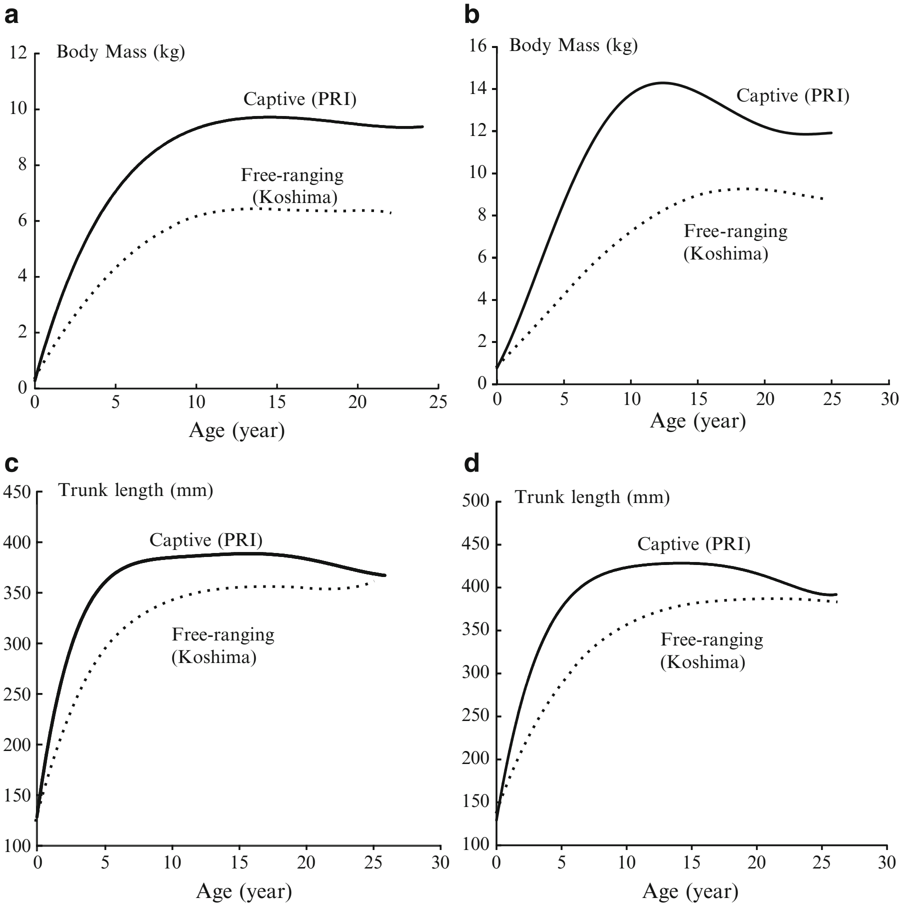

**Fig. 2.12** Age-change graphs of body weight (**a**, females; **b**, males) and trunk length (**c**, females, **d**, males). *Thick lines* indicate the artificially reared group; *dashed lines* indicate the free-ranging group. (From Hamada 2008)

preparation). In the caged group, ages for body weight are from 12.2 and 17.6 years, and 11.2 and 13.9 years in females and males, respectively; in the Koshima group, ages for body weight are 11.6 and 16.3 years in females and 16.7 and 20.8 years in males (Fig. 2.12a,b). Thus, the body weight attained 99% of maximum 1 or 2 years (or several years) later than the starting age of the adult stage, and started decreasing at ages from 14 to 20 years. As for trunk length (Fig. 2.12c,d), in the caged group the ages are 10.0 and 19.5 years in females and 10.3 and 17.8 years in males. In the Koshima group, ages at which 99% of maximum body weight was attained were 10.3 and 15.9 years in females and males, respectively, although trunk length did not decrease in both sexes. Thus, in the caged group the decrease in trunk length, which indicates aging, starts at around 18–20 years of age, but this decrease was not found in the Koshima group. This difference probably occurs because either the macaques in the Koshima group attained the 99% of maximum trunk length much later than those in the PRI group and they would have died before they attained elderly stage, or because an environmental factor (locomotor activity) favored maintaining the trunk length in the Koshima group.

Based on the age changes in vertebrae of Japanese macaques (caged group), it was found that the decrease in height of the vertebral body (craniocaudal diameter) on the abdominal side was greater than that on the dorsal side, and the kyphosis became stronger with age. Macaque individuals older than 15 years of age in the caged group showed kyphosis more or less, and the flexibility of the vertebral column decreased with age from around 15 years, which makes the walking stride shorter and tottering. Vertebral change as well as muscular atrophy and shortening of tendons lessens the movable range of joints in knees or elbows. Similar musculoskeletal and related locomotor changes are common in humans; thus, they can be regarded as an index of aging.

With radiographic observation of the vertebral column (Fig. 2.13), striking aging other than the kyphosis was found, such as osteophytosis, osteoarthritis, and shortening of the intervertebral distance. The vertebral body came to have the shape of those of fish, that is, in the lateral view the diameter at the middle of the vertebral body becomes smaller than the diameters at the cranial and caudal ends (the abdominal contour becomes concave). In parallel with these changes, bone mineral content and bone mineral density in trabecular bone decrease with age and the trabecular bone becomes scarce. Thus, the body tends to experience microfractures, which lead to the smaller diameter on the abdominal side than on the dorsal side of the vertebral body, and the intervertebral disc (cartilage) becomes thinner. In spite of the fact that bone mineral is absorbed from the vertebral body, calcium is deposited anomalously in the joint capsule or intervertebral ligaments. The calcium deposit is first observed in a radiograph as an opaque oval image at the joint, and then it becomes connected to neighboring vertebral bodies (osteophytosis and osteoarthritis; Fig. 2.13). These bone changes start to be observed as early as 10–15 years of age in Japanese macaques, which is reflected by the shortening of trunk length and lessened flexibility of the vertebral column.

The fact that shortening of the trunk was observed in the caged group but not found in the free-ranging group warrants explanation. One possibility is the effect

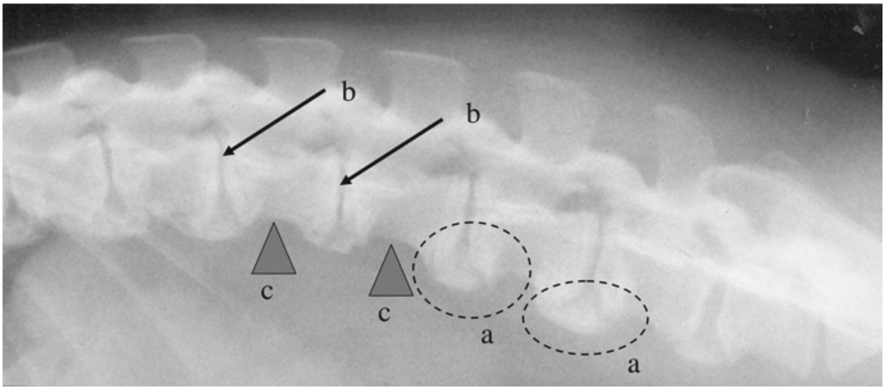

**Fig. 2.13** Lateral view of vertebral column (*left*, cranial side) with kypohosis and aging changes in female Japanese macaque (22.5 years). Osteoarthritis is significantly developed and calcium deposition is found in intervertebral joints (*a*), the interbody distance is short (*b*), and the vertebral body resembles a fish vertebral body shape (*c*). (From Hamada 2008)

of environmental factors such as nutrition and/or locomotor activity on aging in the musculoskeletal system. Being fed nutritionally controlled monkey chow, vegetables, and fruits, macaques in the caged group (PRI) had a rich nutritional supply but their locomotor activity was much more limited. The reverse was the case for macaques in the free-ranging group (Koshima). The preventive effects of nutritional (caloric) restriction on aging are found in various physiological systems both in nonhuman primates and in humans (Weindruch 1996), which should be studied further.

Reproductive aging in caged Japanese macaques can be described by the following stages (Shimizu 2007). Females routinely reproduce offspring until age 17 years; ovarian function starts to decline after about 18 years of age, although the menstrual cycle is still regular until ages 21–25 years, when decline of ovarian function becomes significant. Final birth is at 21.6 years of age on average (SD = 0.4); menopause is experienced at 27 years, showing irregular or loss of menstrual cycle; and the maximum (physiological) lifespan is about 30 years. The interindividual variation is wide, and these ages were obtained from average or long-lived individuals. Statistics obtained from the provisioned group (Arashiyama) showed that females older than 20 years lived for 6 years after the last birth, on average, and considering the duration when females showed menstrual cycles but did not give birth, the postreproductive life was 4.5 years (Takahata et al. 1995). In the early phase of postreproductive life, estrus (swelling and reddening in sexual skin) and mating were found; in the later phase, at about 27.3 years of age, neither of these was exhibited. In the free-ranging provisioned group, which was transferred from Arashiyama to Texas, USA, age at cessation of reproductive activity was about 25 years, with wide interindividual variation (14.5–32.7 years) and the average postreproductive life was 2.1 years on average (Pavelka and Fedigan 1999). Only 2.9% of females lived long enough to experience the cessation of reproductive activity.

From these results, it could be concluded that female Japanese macaques maintained reproductive activity in spite of physical (musculoskeletal system) aging from age 10 to 15 years until about age 25 years and lived another 2–4.5 years without reproduction. In males, mortality before older age (25 years) was much greater than in females, and the reproductive function appeared to be maintained (Hamada, personal observation) In women, aging of the musculoskeletal system starts around 40 years of age, and by the cessation of reproduction (menopause and end of estrogen secretion) physical aging is accelerated, although women have 40–50 years of postmenopausal life (elderly stage; Kaplan et al. 2000). The same physiological changes in the skeletal system that are caused by endocrinological changes was also found in Japanese macaques, although the postreproductive life appeared to be short and was experienced in only a minority of females.

## 2.4 Future of Morphology Studies on Japanese Macaques

The life history pattern of Japanese macaques, especially reproduction and physical aging, is the subject of future study; this pattern should have been inherited from the proto-*mulatta* ancestor and have been shaped by the adaptation to the environment of Japan. We should also determine the morphological consequence of phylogeographical processes that have been elucidated through genetic studies, e.g., extinction of local populations in northern Japan in the glacial period.

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# Chapter 3: Modes of Differentiation in Japanese Macaques: Perspectives from Population Genetics

**Yoshi Kawamoto**

## 3.1 Introduction

### *3.1.1 Genetic Differentiation Between Species*

In bisexually reproducing organisms, individuals in the same reproductive population share common genes. As genes accumulate mutations, genetic differentiation proceeds through time between reproductively different populations. Because of the lack of gene flow after speciation, different species show increased mutational differences, resulting in genetic diversity between species.

Interspecific differentiation is influenced by factors other than mutations. Genes newly derived from mutations are subsequently subjected to selection; where a functionally significant change has occurred, a specific gene can increase even in a short period of evolution. The evolutionary base of organisms has been regarded as such a replacement of adaptive genes to an environment (Dobzhansky 1951). On the other hand, many molecular-level mutations are considered to be selectively neutral and follow a random process of fixation that is approximately proportional to evolutionary time (Kimura 1983). Thus, genetic distance measured by protein or DNA scales generally reflects the time after splitting from the common ancestor between species.

### *3.1.2 Genetic Differentiation Within Species*

Every organism on earth shows genetic differentiation, both between and within species, which results from environmental causes in different localities or the population

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structure of the species. The main interest of this chapter is the cause and structure of intraspecific differentiation of Japanese macaques (*Macaca fuscata*).

The causes underlying intraspecific genetic differentiation are not necessarily related to the genetic bases of evolutionary adaptation in a species; they can be associated with the process of species formation or genetic changes correlating with environmental changes in habitats. In this chapter, I review the genetic diversity and local differentiation in Japanese macaques to discuss the structure of genetic differentiation in nonhuman primates and its causes.

### *3.1.3 Genetic Differentiation of Primates*

Extant species of primates show great diversity in their social structure (Itani 1972). Japanese macaques form a multimale–multifemale social group and exhibit a typical matrilineal society that is founded on the maternal bond of individuals. Conversely, chimpanzees (*Pan troglodytes*) live in a typical patrilineal society, where males maintain bonds in a group. In general, the characteristics of intraspecific genetic differentiation are variable among primate species because of the differences in both social structure and evolutionary history (Kawamoto et al. 2007a). Japanese macaques can represent a good model in studies focusing on the relationship between evolutionary and genetic changes because they have been investigated across many research fields and provide good sources of relevant information to discuss the causes of differentiation within species.

## 3.2 Diversity and Geographical Differentiation in Nonmolecular Traits

### *3.2.1 Morphological Traits*

The pelage color of Japanese macaques shows typical changes according to environmental conditions, with hair becoming brighter in the northern habitat range. Such changes are known as Gloger’s rule (Hamada et al. 1992; see Fig. 2.4 in Chap. 2). The pelage color of infants less than 4 months old is darker than that of older individuals, particularly in the population on Yakushima Island (Kuroda 1984; Hamada 2002; Fig. 3.1). The density of body hair correlates with climatic or environmental condition, with populations inhabiting snowy or colder areas exhibiting higher density (Inagaki and Hamada 1985; see Fig. 2.2 in Chap. 2).

Individual variations in dermatoglyphics indicate a slight difference in the occurrence of qualitative patterns, in which populations in Shimokita Peninsula and Yakushima show constitutional deviation from those in other areas (Iwamoto and Suryobroto 1994).

**Fig. 3.1** Geographical map for locations cited in Chap. 3, including islands, regions, and peninsulas. *Solid triangles* indicate excavation sites of fossils

In terms of body size, standard measures such as crown-rump length, sitting height, and body weight gradually increase from Yakushima to Honshu Island, as expected from Bergman's rule. Within populations on Honshu, however, such gradual changes are not obvious for crown-rump length and sitting height but are for body weight. When compared to mean temperature in January instead of latitude, the correlation becomes higher in the Honshu populations; this could result from adaptation to cold climatic conditions (Hamada 2002; Hamada et al. 1996, see also Fig. 2.1 in Chap. 2). Smaller body size has been observed in the populations of Boso Peninsula and Kinkazan Island in and around Honshu (Hamada et al. 1996; Mouri and Nishimura 2002). For tail-related characters, such as tail length and relative tail length (proportion of tail length to crown-rump length), latitudinal cline is not remarkable, where the populations on Yakushima and Shodoshima Island are relatively large and those on Koshima Islet are small (Fooden and Aimi 2005). For cranial measures, maximum head length tends to increase from Yakushima to

Kyushu Islands, as expected from Bergman's rule, but such trends are not obvious on Shikoku and Honshu (Fooden and Aimi 2005). Similarly, in cranial size, the populations in Boso and Kinkazan are smaller than those in other areas (Mouri and Nishimura 2002). Based on a craniomorphometric study of adult females, Mouri and Nishimura (2002) found that populations inhabiting the peripheral range of the species distribution, such as on Yakushima, Boso, and Kinkazan, are likely to deviate from those in the center of the distribution. This trend is consistent with a morphological study on dental traits (Yamamoto 2007).

### *3.2.2 Reproductive Traits*

Japanese macaques are seasonal breeders. Local difference in birth season has been observed since the early field studies (Kawai et al. 1967). The mean peak season is generally early in the north and late in the south, but exceptions are known in marginal populations: late in the northernmost Shimokita population and early in the southernmost Yakushima population. These marginal populations significantly deviated from linearity in mean birth season with latitude of habitat (Fooden and Aimi 2003; Fig. 3.2).

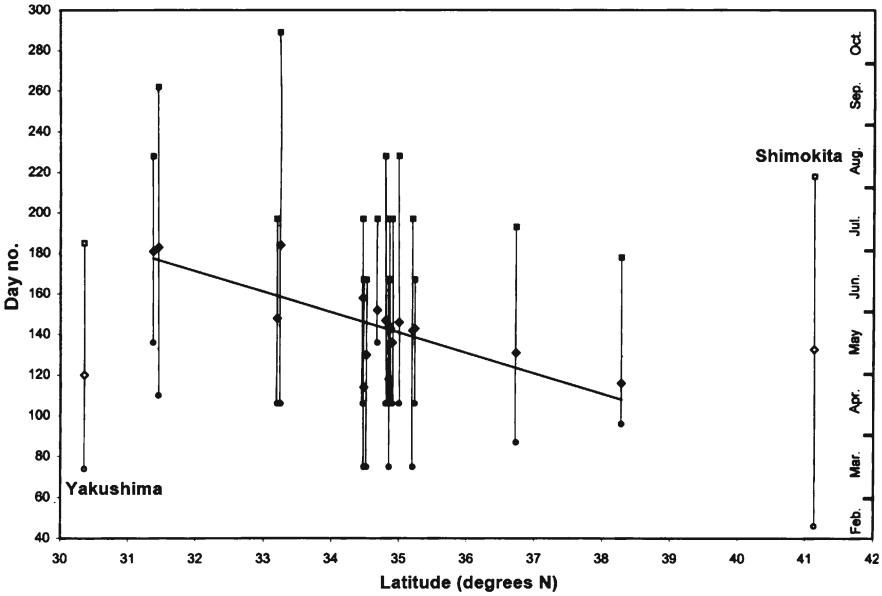

**Fig. 3.2** Relationship between birth seasonality and locality of habitats. (From Fooden and Aimi 2003). The *abscissa* is latitude; *right and left ordinates* indicate calendar scale and days after January 1, respectively. Here, a total of 18 groups are compared for the dates of earliest, average, and latest time of birth

### 3.2.3 Ecological Traits

Home range size and group size vary in Japanese macaques depending on the vegetation type of the habitats (Takasaki 1981). The home range per animal is smaller in evergreen forests than in deciduous forests (see Fig. 4.5 in Chap. 4). In broad-leaved forests, the size of the habitat range usually correlates with the size of a natural broad-leaved forest, but populations in the Tohoku Region and Niigata Prefecture show a smaller range size, probably because of the influence of hunting pressure (Koganezawa 1991).

### 3.2.4 Modes of Differentiation in Nonmolecular Traits

We overviewed diversity and differentiation of nonmolecular traits in Japanese macaques. The characteristics of local differentiation can be categorized into three distinct modes. The first mode (mode I) is a gradual change associated with climatic or physical conditions within habitats, known in terms of Bergman's rule or Allen's rule. In Japanese macaques, a typical association has been observed in changes with latitude or temperature in winter. The continuous change in traits is not necessarily clear over entire habitats, and such a tendency is less clear on Honshu Island.

The second mode (mode II) is a contrast between geographically central and peripheral habitats associated with isolation on an island or a peninsula. This is a discontinuous change that appears in the peripheral zone of distribution, such as regions of Koshima, Boso, Yakushima, Shodoshima, and Kinkazan, where populations are isolated by water gaps of the sea or a river system.

The third mode (mode III) is a change associated with environmental or vegetation conditions in habitats: this is also a discontinuous change but it differs from that in mode II. The change is related not to the geography (location) of habitats but to the environmental or ecological conditions.

## 3.3 Molecular Genetic Approach to Diversity and Geographical Differentiation

### 3.3.1 Molecular Genetic Markers

Diversity in the social structure of primates reflects the variety in life history of males and females. In the case of Japanese macaques, we can observe the typical matrilineal organization of social groups in the population, where females live in their natal places but males disperse when sexually mature (Nishida 1966). Although one long-term study of Japanese macaques recorded female emigration from the natal group (Sugiyama and Ohsawa 1982), this seems to be rare in the species.

Female philopatry and male-biased dispersal form the basis of genetic structuring in Japanese macaque populations. It is doubtless true that males regulate gene flow between populations. If the transfer of males with neighboring populations is interrupted, the population will become isolated genetically and then show molecular and nonmolecular differentiation from other populations. Therefore, adult male transfer is a key to discussing local differentiation. A social group of Japanese macaques consists of multiple maternal lineages. A social group is a basic unit of local populations, and its demographic change is associated with fission by increase in size or fusion by decrease in size (Takahata et al. 1994). When group fission happens, it results in an unequal split of maternal lineages in the group (Furuya 1969; Koyama 1970). The historical changes in geographical distribution of the species are associated with the rise and fall of maternal lineages in social groups (Kawamoto et al. 2007a).

In relationship to socioecological characteristics, the application of different sex-related genes is important for understanding the diversity and differentiation of Japanese macaques. Bisexual markers such as autosomal genes, equally contributed by both parents, are valuable to evaluate gene flow by adult male transfer between social groups. Y-chromosome genes are also useful in the direct monitoring of male-mediated gene flow. Mitochondrial DNA (mtDNA) is of particular interest as a molecular marker in the population genetics of Japanese macaques. As this marker is maternally inherited and rapidly evolving, it is applicable for understanding the changes in matrilineal units in populations. Those changes could be a good indicator of the evolutionary history of geographical distribution in the species via group fission and subsequent population expansion. The application of mtDNA markers to adult males could have a different context. As males do not transfer their mtDNA types to the next generation, the marker can be used for the monitoring of male dispersal in ecology but not for the monitoring of gene flow.

Specific features of Japanese macaques, such as differences in life history between males and females, multimale–multifemale structure of groups, and matrilineal sorting in group fission, present a unique approach in population genetics study. The use of a set of different sex-related marker genes can provide important information on the ecology, evolution, and conservation of the species.

### *3.3.2 Definition of Local Population*

It is necessary to define the population unit in research before discussing the population genetics of Japanese macaques. A standardization of population units is needed for comparative studies, not only in genetics but also in other research fields. This approach is particularly important in mammalian studies that compare differences in locality within species. In Japanese macaques, social groups are commonly considered as a basic unit of comparison. Social groups are visible units in nature, and we can evaluate their spatial distribution and movements unquestionably by direct observations and a global positioning system (GPS). Based on the obtained records of moving ranges, we can evaluate the geographical continuity of the distribution and can define arbitrarily their meta-population by assuming criteria that have a sound biological basis. In a population genetics study, such an empirical definition can be adopted as a first choice, because a social group of macaques is the basic unit of reproduction and its size and distribution are major factors determining the genetic structure of a population.

Conservation studies of Japanese macaques have applied a definition of local population based on the geographical continuity of group distribution. Researchers and officers commonly use the national census map that plots group distribution within a 5-km$^2$ mesh (Ministry of the Environment 2004). In traditional population management practices, those groups which inhabit the same island but are separated more than three meshes (15 km) apart are defined as belonging to a different meta-population (local population; e.g., Koganezawa 1995; Ministry of the Environment 2004). In contrast, as explained later (Sect. 3.4.2), the concentration of social groups more than 100 km apart is treated separately based on correlation analysis between geographical and protein genetic distances (Kawamoto et al. 2008).

## 3.4 Diversity and Geographical Differentiation in Genetic Traits

### *3.4.1 Morphogenetic Characters*

Little is known about the genetic background of morphological variation in Japanese macaques. Long-term observation of Japanese macaques has occasionally disclosed morphological mutants in natural populations. Two traits have received extensive attention from primatologists in Japan: congenital limb malformation and color variation in the coat or eyes. In the 1970s, malformations of fingers or limbs occurred frequently in many parts of Japan, including so-called “monkey parks” where macaques were intensively fed to promote tourism, and for the populations in Awajishima Island, Kyushu, and Honshu (Yoshihiro et al. 1979; Nakamichi et al. 1997; Turner et al. 2008). No major cause of these malformations was found from surveys on residual pesticides, karyotype abnormality, or pedigree analysis in genetics (Shidei 1984; Minezawa et al. 1990; Nozawa et al. 1996).

Pelage color variations have been reported sporadically in Japanese macaques. Among these are the famous whitish macaques that live in the mountain district near the border between Yamagata and Fukushima Prefectures in Tohoku Region. Although their mutational background is not known, individuals in groups living in the snowy area have a brighter pelage (Endo 1978; Nozawa et al. 1996). Individuals with bluish eyes have been observed in Shodoshima and Kyushu Islands (Zhang and Watanabe 2007) and in an exported population from Honshu (Masataka 1982), but their mutational background is also unknown.

### *3.4.2 Autosomal Markers: Protein Genes and Microsatellite DNA*

Protein polymorphisms are well analyzed in Japanese macaques. Studies have been conducted since the early 1970s by Ken Nozawa and his colleagues; they have screened about 30 protein loci for many groups or local populations (Nozawa et al. 1975, 1982; Shotake 1974; Shotake and Nozawa 1974; Shotake and Ohkura 1975; Shotake et al. 1975, 1977; Hayasaka et al. 1987). Protein alleles do not show uniform distribution throughout habitats. Localization of specific alleles is obvious in the molecular markers (Fig. 3.3). Genetic variability within groups is low in Japanese macaques (Nozawa et al. 1982, 1991) compared to those of long-tailed macaques

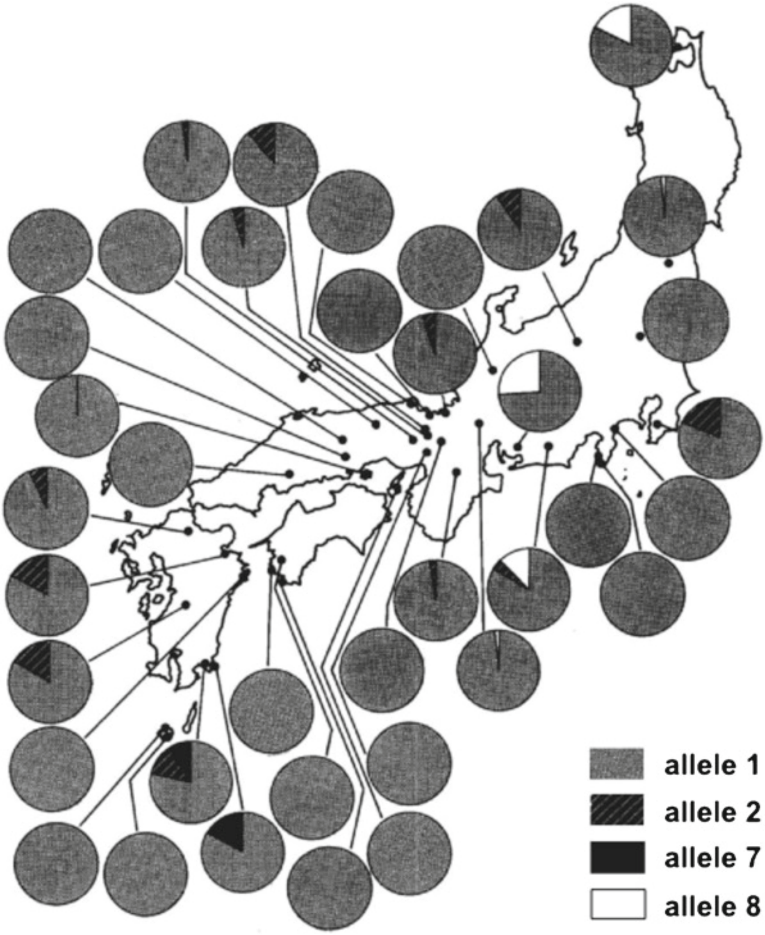

**Fig. 3.3** Geographical distribution of blood protein polymorphism in Japanese macaques. (From Nozawa et al. 1991). This map illustrates frequency differences in four alleles at the glucosephosphate isomerase locus following examination of 3,409 individuals from 38 localities

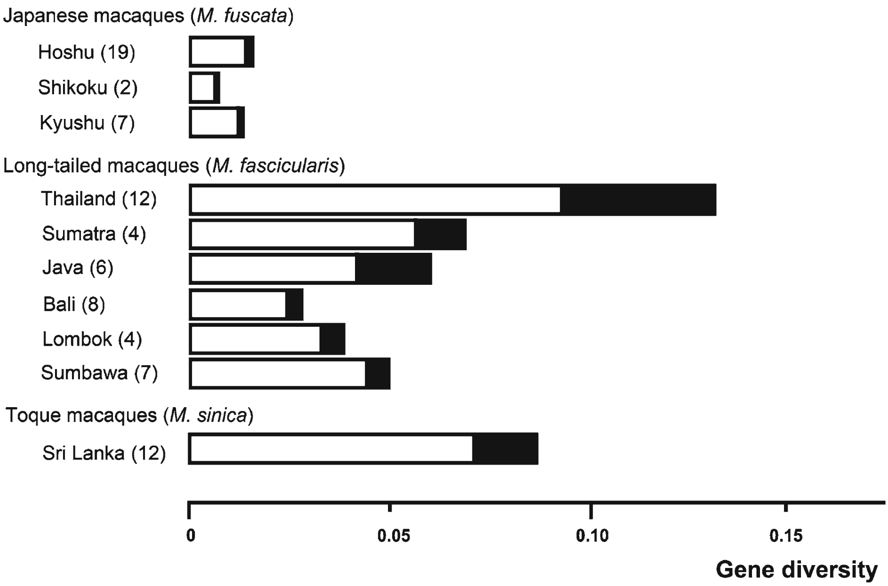

**Fig. 3.4** Comparison of gene diversity in Japanese macaques, long-tailed macaques, and toque macaques. The diversity was quantified by blood protein variations for each geographically distinct population in the species. The *figures in parentheses* are the number of social groups sampled. *White* and *black bar segments* indicate the gene diversity attributed to components within and between groups in the population, respectively

(*Macaca fascicularis*) in Indonesia and Thailand (Kawamoto et al. 1984, 1989) and toque macaques (*Macaca sinica*) in Sri Lanka (Shotake et al. 1991; Fig. 3.4). Both absolute and relative gene diversities between groups are very low in Japanese macaques, as indicated by the width and proportion of blackish portions in Fig. 3.4, respectively.

Statistical analysis between genetic and geographical distances showed that two social groups more than 100 km apart were not significantly correlated. Thus, groups far apart can be regarded as genetically independent (Nozawa et al. 1982). Cluster analysis using protein genetic distances between social groups (or groups of neighboring social groups) revealed remarkable differentiation of island populations (Yakushima and Shodoshima) or peninsular populations (Shimokita and Boso) in the periphery (Nozawa et al. 1991; Tomari 2003; Fig. 3.5).

Species-scale investigation has not been summarized for microsatellite DNA polymorphisms. Available reports on social groups or local populations generally support the trend found in blood protein studies (Shotake and Yamane 2002); however, contradictory results were obtained in a few cases. The population of Shimokita, the northernmost habitat of the species, was previously reported as being highly polymorphic in protein markers (Hayasaka et al. 1987), but reassessment by autosomal microsatellite markers revealed lower heterozygosity of the same population (Kawamoto et al. 2008). The causes of this contrast are considered to be

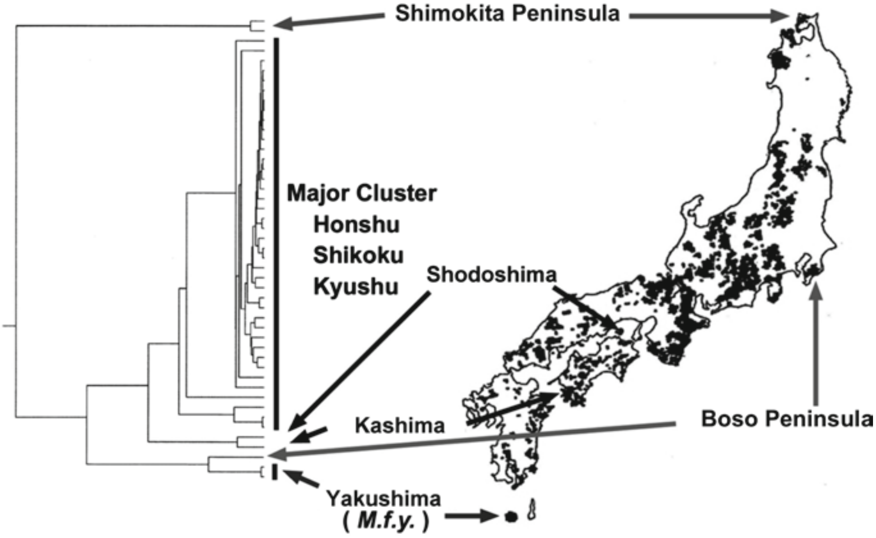

**Fig. 3.5** Genetic differentiation in Japanese macaques inferred from blood protein variations. (From Tomari 2003). *Right*: Map showing the distribution of social groups in the Japan archipelago (Ministry of the Environment 2004) with a special indication of habitats in the periphery. Here, the Kashima Island population is not naturally distributed, but has been introduced by humans. *Left*: A dendrogram constructed by the UPGMA method following screening of 30 blood loci for 3,676 samples from 47 localities

the differences in mutation rate of markers used in the study and biases in locus sampling in the evaluation of genetic diversity (Kawamoto et al. 2008).

Although there is a local contrast, the mode of genetic differentiations are generally similar between nuclear autosomal markers, indicating less diversity among groups or local populations in the geographically central habitats of Honshu, Shikoku, and Kyushu, with degrees of genetic variability that are not significantly different within populations. Conversely, populations in the geographically peripheral regions, such as Shimokita, Boso, and Yakushima, are greatly differentiated. This mode of local differentiation is a mode II category.

### *3.4.3 Mitochondrial Genes*

There is a contrast in the mode of local differentiation between mtDNA and other genetic markers in Japanese macaques. This difference can be typically recognized in the geographical distribution pattern of certain gene types in the habitats. In mtDNA variations, the members of each social group can be characterized by a very small number of haplotypes. By excluding adult males as possible emigrants from different groups, each group of Japanese macaques can be characterized by one or a few mtDNA haplotypes in a phylogeographical assessment (Kawamoto et al. 2007a), which could result from a limited number of composite matrilines in the groups and their close relationship in pedigrees.

Nucleotide sequencing of the noncoding region of the mitochondrial genome has been used in population genetics studies of Japanese macaques (Hayasaka et al. 1991; Kawamoto et al. 2007a). This part of the genome is rapidly evolving and easy to screen in natural populations. We can apply blood, saliva, hair, and fecal samples for the assessment of mtDNA haplotypes (Hayaishi and Kawamoto 2006; Kawamoto et al. 2008).

Kawamoto et al. (2007a) investigated a total of 135 groups by partial sequencing (412 bp) of the noncoding region. They examined only female samples to avoid the influence of migrant males in the study. A total of 53 mtDNA haplotypes were detected, and the mode of local genetic differentiation was evaluated by means of molecular phylogenetic and population genetics analyses. The study disclosed a unique phylogeographical structure in the species. The clustering analysis revealed two major groups of populations, those in the eastern and western parts of the habitats. They were bordered between the Kinki and Chugoku Regions on Honshu (Fig. 3.6).

Close observations of the two mtDNA haplogroups suggest that there are two subgroups in the eastern group, those in Kii Peninsula and the other areas (A2 and A1, respectively, in Fig. 3.6). There are three subgroups in the western group. Conspicuously, one of the subgroups in the western group includes a subset of haplotypes that is distributed in east Japan, but not in west Japan, covering part of the Kanto Region (B1 in Fig. 3.6). Those haplotypes were grouped together in the western haplogroups in the molecular phylogenetic tree (Fig. 3.6). The two haplogroups depicted from the mtDNA phylogeography differ in the features of their molecular diversity. The western haplogroup indicates large diversity where the tree length between composite haplotypes is relatively longer than those of the east (Fig. 3.7). This finding means that the populations in the west lack intermediate types in their mtDNA haplotype network. Conversely, a number of composite haplotypes exist in the east, and the nucleotide diversity between haplotypes is smaller than those in the western haplogroup. This result is not caused by sampling biases, as the study covers the whole distribution range of the species. Statistical analysis of genetic diversity suggested that there was a significant ancient population expansion in the eastern habitats of Japanese macaques (Kawamoto et al. 2007a).

The characteristics of local genetic differentiation found in mtDNA phylogeography suggest that the populations living in western part of the habitats are historically older than those in the east. This contrast in Japanese macaques is discussed by assuming the contraction of habitats to the western area at the time of last glacial period (about 20,000 years ago) and postglacial population expansion to the eastern area after the termination of the period (since 10,000 years ago; Kawamoto et al. 2007a).

The findings obtained from mtDNA phylogeography could result from changes in distribution areas in the evolutionary history of the species, and those changes

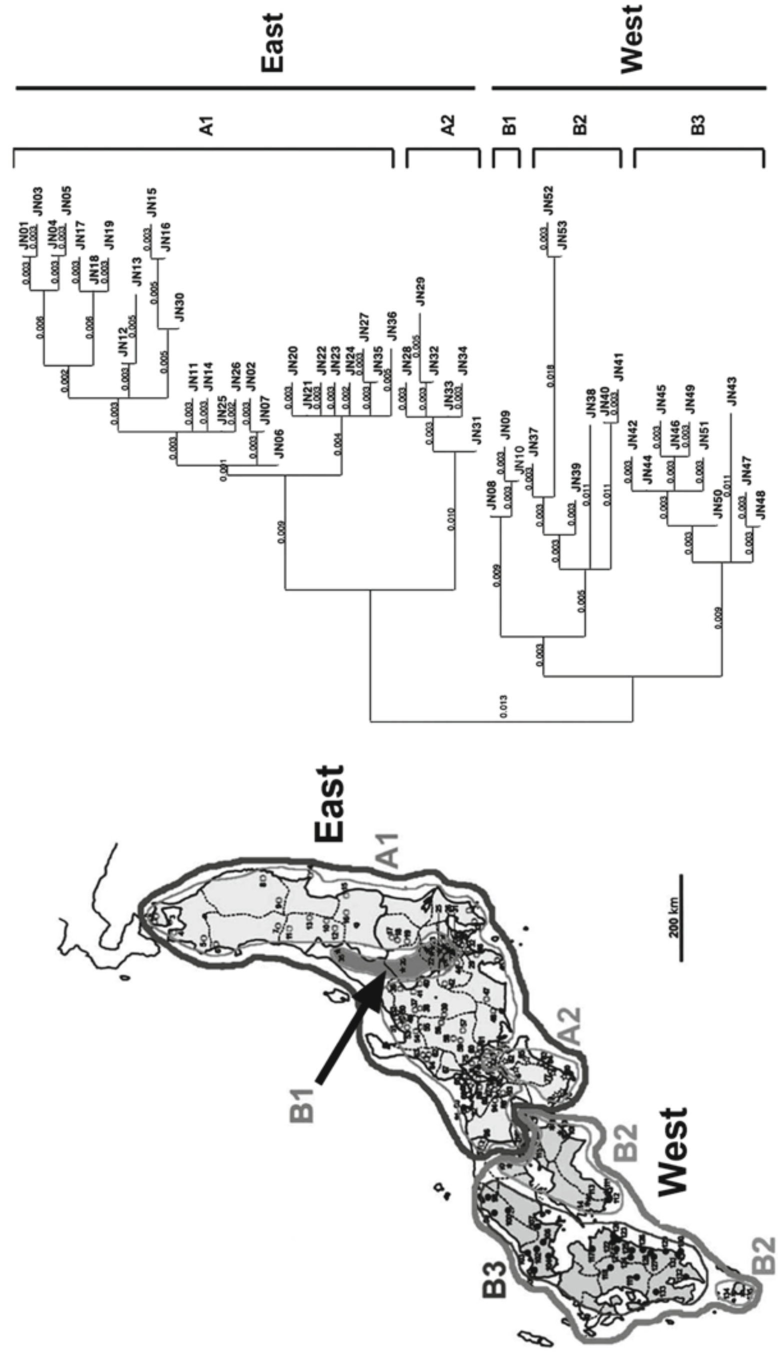

**Fig. 3.6** Genetic differentiation of Japanese macaques in mtDNA. (From Kawamoto et al. 2007a). *Right*: Phylogenetic tree of mtDNA haplotypes showing two major clusters in Japan. *Left*: Map showing the geographical distribution of major haplogroups in the east and west of habitats. The east haplogroup has two subgroups (A1 and A2); the west haplogroup has three subgroups (B1, B2, and B3)

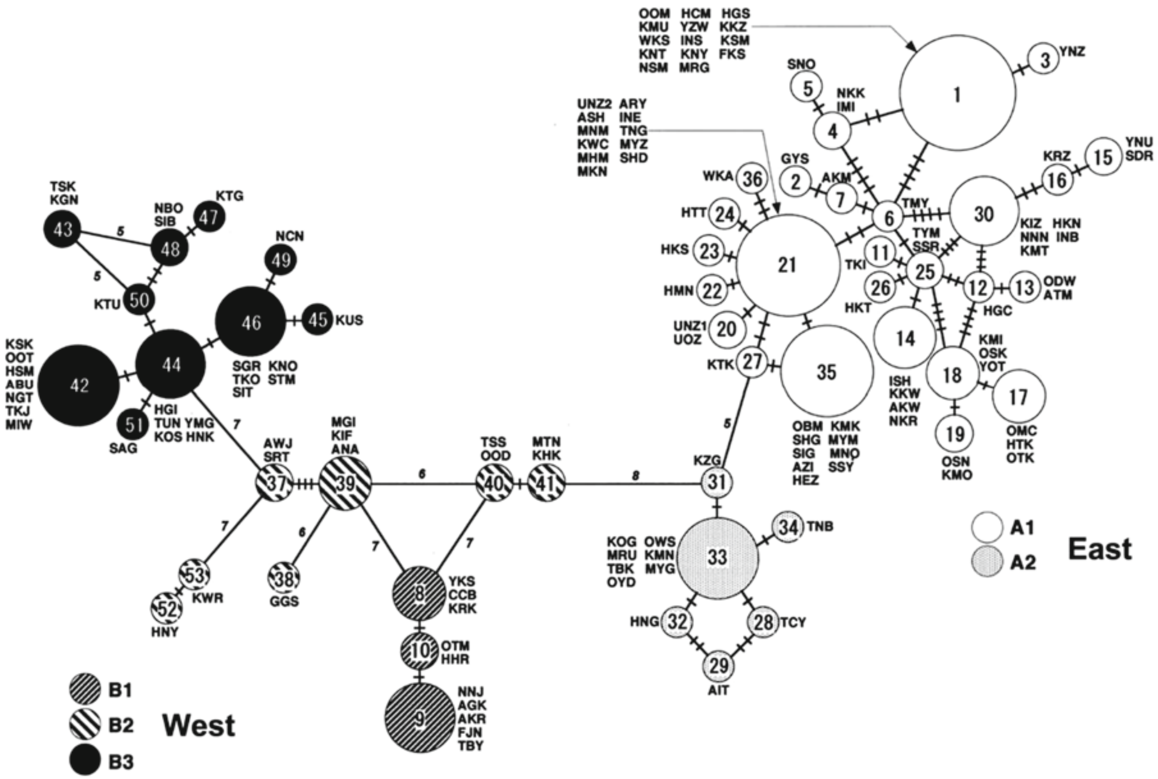

**Fig. 3.7** A minimum spanning network showing frequencies of haplotypes (proportional to the size of the circle) and mutational differences between mtDNA haplotypes found in Japanese macaques. (From Kawamoto et al. 2007a). *Numbers in the circles* indicate the names of mtDNA haplotypes. East and west haplogroups are further categorized into subgroups using different shadings

are likely to be reflected in the diversity and local differentiation of the maternally inherited marker in Japanese macaques. This mode of differentiation is type III and apparently different from the mode found in autosomal markers.

### *3.4.4 Y-Chromosomal Genes*

Genes on the Y chromosome are paternally inherited in mammalian species. As most of the genes are not functionally important, they have not been characterized as have other chromosomal genes. Individual variations of the Y chromosome provide significant information in evolutionary and ecological studies in primatology, but the development of available tools is not advanced. As a result of the recent progress in genome studies, microsatellite DNA polymorphisms have been investigated in humans and great apes. For humans, 166 Y-microsatellite loci have been confirmed (Kayser et al. 2004), and their polymorphisms have been reported in various countries or tribes (Qamar et al. 2002; Zerjal et al. 2003). Homologues of the Y-marker loci developed in humans are similarly applicable to the study of great apes (Erler et al. 2004). Microsatellite DNA variations on the Y chromosome have been studied in wild populations of bonobo (*Pan paniscus*; Eriksson et al. 2006) and gorilla (*Gorilla gorilla*; Douadi et al. 2007).

The applicability of human markers decreases in nonhuman/nonape primates in relation to their phylogenetic proximity (Erler et al. 2004). We have found three loci (DYS472, DYS569, and DYS645) that show polymorphisms in different individuals of Japanese macaques. Those markers consistently give a single polymerase chain reaction (PCR) product in males and none in females, as they are located on the nonrecombining part of the Y chromosome. We can define different types of the chromosome by comparing composite haplotypes given by the combination of allele types. We have discriminated nearly 70 Y haplotypes in Japanese macaques (Kawamoto et al., unpublished data).

An application of molecular analyses to the population study in the Tohoku Region revealed genetic isolation of the population on Shimokita, the northernmost range of the species. Low genetic diversity in Shimokita and its great differentiation from other local populations were revealed by multilocus screening of microsatellite markers on autosomes and Y chromosome (Fig. 3.8; Kawamoto et al. 2008). The mode of differentiation was highly correlated between the two sets of nuclear markers, but the mode of the mtDNA marker contrasted with the nuclear markers. The Goyosan population in the Tohoku Region suggested an opposite case to the Shimokita population in the study. The Goyosan population is small in size and geographically isolated (Fig. 3.8). It shows specific mtDNA haplotype contrasts with those in surrounding populations (Kawamoto et al. 2007a). However, its genetic diversity is greater than that of the Shimokita population in microsatellite DNA markers, including Y-chromosome markers (Kawamoto et al. 2008). This observation suggests that male transfer has a prominent role in preventing genetic isolation of the Goyosan population from its neighboring populations.

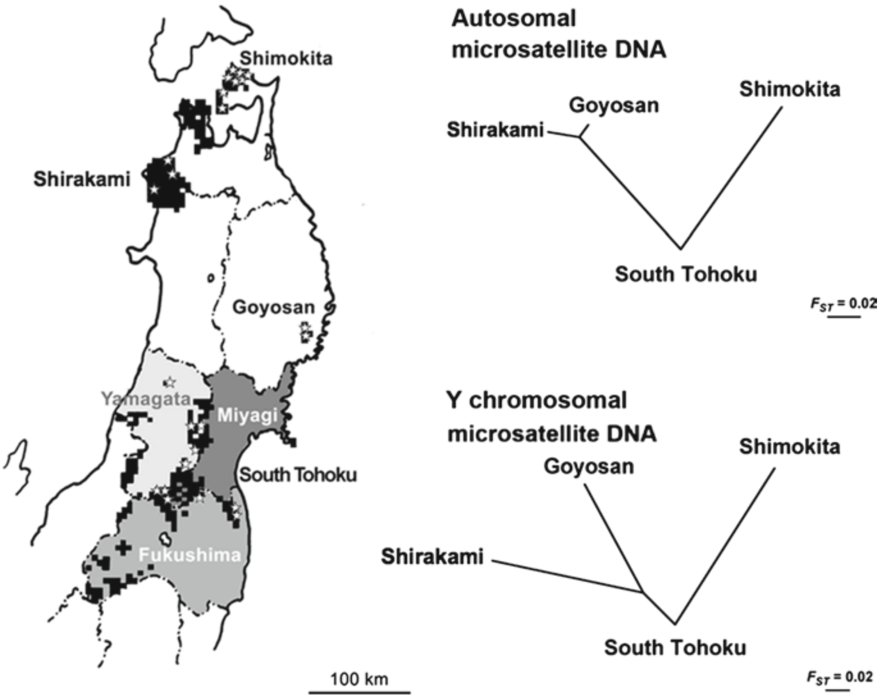

**Fig. 3.8** Populations in the Tohoku Region investigated for genetic differentiation using microsatellite DNA. Six local populations located more than 100 km from each other were examined for autosomal and Y-chromosomal markers. (From Kawamoto et al. 2008). *Right*: Trees showing diversity between study populations quantified by $F_{ST}$ distances from 11 autosomal loci (*above*) and 3 Y-chromosomal loci (*below*). *Left*: Map showing the study populations. *White star* marks the sampling locality

Consequently, the mode of differentiation in Y-chromosomal genes is related to the dispersal and reproduction of adult males. The genetic differentiation follows mode II of local differentiation, at least for populations in the Tohoku Region. We need confirmation of this by further investigation of other local populations.

## 3.5 Mechanism of Local Genetic Differentiation

### *3.5.1 Cause of Genetic Differentiation*

The mode of inheritance, dispersal patterns in relationship to social life, and molecular evolutionary characteristics all relate to the observed difference in the mode of local differentiation of molecular genetic markers. In particular, sex specificity in the inheritance mode together with female philopatric behavior produces remarkable contrast between mtDNA and nuclear markers. It is inferable that the effective number of females, in terms of contribution to regeneration of populations, is relatively small in the social groups of Japanese macaques. The maternal lineage sorting at the moment of group fission accompanied with population bottleneck effect suggests that the fixation rate of mtDNA haplotypes could be high in the social groups. This inference is supported by low mtDNA diversity within groups and geographical clusters of mtDNA haplotypes in Japanese macaques.

The observed correlation between autosomal and Y-chromosomal markers suggests that total gene diversity in the nuclear genes is governed mainly by gene flows borne by male migrants between social groups. This interpretation further suggests that the significant change in ecological conditions that prevents interlocal gene flows will result in local differentiation of species. The peripheral habitats of Japanese macaques, such as Shimokita, Boso, and other small islands, are considered to be cases of local isolation, mainly for geographical and other environmental reasons. Conversely, impact on wildlife populations from human activities, such as traditional hunting for meat, skins, and medicine, vegetation change by plantations, and pest control, can be a cause of local isolation of populations. In the case of Shimokita, Kawamoto et al. (2008) tested the impact of recent hunting pressure on the population. Although they found a decrease in genetic diversity in the population, the result did not support recent impact, but rather an ancient bottleneck probably soon after population expansion in the postglacial period. That study indicates that ecological condition is not always the sole factor of local differentiation, and that evolutionary background can be a major cause of such differentiation. Results from population genetic studies of Japanese macaques highlight the applicability of various molecular tools and show perspectives of their use in conservation genetics.

### *3.5.2 Lessons from Interspecific Hybridization in Japan*

The correlation of differentiation between autosomal and Y-chromosomal genes, resulted from intergroup male transfer, was proven by evidence from studies on native and alien macaque populations in Japan that accidentally hybridized. Such studies were done in Wakayama Prefecture (Kawamoto et al. 1999, 2001; Kawamoto 2005) and Aomori Prefecture (Kawamoto et al. 2005) for hybrids between Japanese and Taiwanese macaques, and in Chiba Prefecture (Hagihara et al. 2003; Kawamoto et al. 2004, 2007b) for hybrids between Japanese and rhesus macaques. Apart from one ambiguous incidence in Chiba Prefecture, no immigrant female of Japanese macaques was detected in the hybrid groups from mtDNA screening of the birthplaces. The results indicate that the hybridization was initiated by crosses between immigrant males of Japanese macaques and residential females of the alien species (Kawamoto et al. 2007b).

## 3.6 General Discussion

### *3.6.1 Habitat Conditions and Genetic Differentiation*

In the evolution of nonhuman primates, the ancestors of Japanese macaques adapted to cold environmental conditions and then finally reached an archipelago in far-eastern Asia. The attainment point is located in the northernmost range of the current world distribution of nonhuman primates, and they have been living in different climatic conditions from the tropics. The distribution area has been located at one of the cold fronts in the evolutionary history of primates, and they have existed up to date although those other cold fronts were previously occupied by colobines that had been exterminated (Iwamoto et al. 2005). It is inferable that climate or vegetation changes at such a cold front strongly influenced the local differentiation of Japanese macaques. Similarly, geological changes and natural disasters could have played a significant role in the spatiotemporal changes in the environment conditions. Recent human impact is another possible cause of the local differentiation. Those environmental factors are involved in the current status of local populations of Japanese macaques.

Adaptation to cold environments of Japanese macaques extends to a latitude of 41°30′N (Aomori Prefecture) and up to 2,360 m a.s.l. (Nagano Prefecture; Izumiyama et al. 2003). When seasonal migration in summer is considered, macaque habitats extend to a summit above 3,000 m a.s.l. in the central mountainous regions of Honshu Island (Izumiyama 2002; Fig. 3.9). They even live in the snowy environments of mountainous or northern areas where temperatures fall below –20°C in winter. Adaptation to current cold environments is reflected well in some of the nonmolecular traits categorized in mode I, but the molecular traits reviewed in this chapter do not simply exhibit such a mode of local differentiation.

The molecular genetic markers used here, probably being selectively neutral (Nozawa et al. 1982), suggest different aspects of evolutionary change in Japanese macaques. Diversity in vegetation and geological tectonics in Japan could have influenced genetic differentiation in Japanese macaques. Those influences seem to appear strongly in the mtDNA phylogeography. Despite the small landmass of Japan (372,000 km$^2$), floral diversity ranges from subtropical to subalpine (Yoshioka 1973; Kira et al. 1976), with forest being the dominant vegetation type in most areas because of the high precipitation throughout the year. Vegetation in these zones provides two primary habitats for Japanese macaques: warm-temperate evergreen broad-leaved forest in the southwestern range, and cool-temperate deciduous broad-leaved forest in the northeastern range (Uehara 1975). If the observed features of mtDNA phylogeography strictly follow the philopatric nature of female and matrilineal lineage sorting of past group fission, the sign of population expansion detected in the mtDNA study suggests that the establishment of ancestral populations occurred earlier in the west than in the east. The recent expansion in the east is also supported by the haplotype distribution pattern in the northernmost range, the Tohoku Region, where mtDNA diversity is

**Fig. 3.9** A group of Japanese macaques feeding at an alpine zone (about 2,600 m a.s.l.) in Nagano Prefecture in summer. (Photograph by Y. Kawamoto)

exceptionally low and establishment of the population is postulated to have been recent, probably at a late period of the postglacial expansion in east Japan after the last glacial maxima. As mtDNA diversity caused by population fragmentation or isolation by distance was unlikely, this homogeneity of mtDNA variation could indicate that the population in that area was established over a short period of time, one too short in which to accumulate a number of new mutations. At present, the populations in that region are very fragmented (Mito 1992; Ministry of the Environment 2004). Genetic differentiation in mtDNA is unusually low in the geographically peripheral areas of the northernmost range of Japanese macaques, and this suggests a scenario in which ancestral populations only recently expanded to most areas in east Japan. Consequently, the great differentiation observed in the nuclear genes on Shimokita could be explained by population bottleneck accompanied with geographical isolation at the moment of postglacial warming (Kawamoto et al. 2008).

Similar association between habitat changes and genetic differentiation in short evolutionary time could be considered for Boso, where the populations have experienced geographical isolation since the rise in sea level at the time of postglacial warming about 6,000–7,000 years ago (Japan Association for Quaternary Research 1987).

Meanwhile, the Yakushima population (*M. fuscata yakui*) experienced extremely reduced genetic diversity in proteins (Nozawa et al. 1991) and mtDNA (Hayaishi and Kawamoto 2006), probably the result of an ancient natural disaster. The past population crash is inferable for the island, where an eruption of pyroclastic flows about 7,000 years ago could have had a significant impact on differentiation in addition to preceding geographical isolation from other regions (Hayaishi and Kawamoto 2006).

Additionally, human activities have changed the habitat conditions of Japanese macaques. Hunting and forest habitat modification are presumed to have considerable impact on the local genetic differentiation; however, its impact has not been well qualified to date.

### *3.6.2 Evolutionary History and Genetic Differentiation*

From a postulated oldest fossil record of the macaque lineage discovered in the Ando quarry, Yamaguchi (Iwamoto and Hasegawa 1972; see Fig. 3.1), the ancestors of Japanese macaques are regarded to have reached the archipelago from the continent through the Korean Peninsula at latest 0.43–0.63 million years ago (MYA; Aimi 2002). The distribution of their ancestors is considered to have covered the whole of Honshu Island before the last glacial maxima (15,000–25,000 years ago). This date is suggested from a fossil canine, estimated at 0.12 MYA (Aimi 2002), excavated from the northernmost part of Honshu, Cape Shiriyazaki in Aomori Prefecture (Iwamoto and Hasegawa 1972; Fig. 3.1).

Two hypotheses have been presented for the establishment of Japanese macaques on the archipelago. Nozawa et al. (1991) discussed the possibility of a two-wave immigration of ancestors into Japan, based on the diversity and differentiation in protein variations. In the scenario, they assumed in the historical sequence that the first wave of immigrants dispersed across the entire area with a high frequency of a certain protein allele, such as the type 2 allele at the phosphoglucomutase II locus that specifically occurs presently in the peripheries of Shimokita, Boso, and Yakushima. The second wave of immigrants carried those alleles commonly found at present in the geographically central habitats in the main islands.

In contrast, Kawamoto et al. (2007a) discussed the origin of Japanese macaques by assuming a single event of immigration from the Asian continent. They regarded that the great differentiation of nuclear genes in the periphery could be explained in terms of a population bottleneck after the last glacial period, and presented supporting evidence to that hypothesis for the Shimokita population (Kawamoto et al. 2008) and the Yakushima population (Hayaishi and Kawamoto 2006).

Future studies on the evolutionary history of Japanese macaques need to test for the contradiction in the two hypotheses. The modes of genetic differentiation observed in Japanese macaques should be related not only to the current conditions in population structure of the species but also to the history of local populations.

### 3.6.3 Perspectives of Study on Japanese Macaques

An overview of local differentiation in molecular and nonmolecular traits has presented three distinctive modes in Japanese macaques. Small but diverse habitats in the archipelago are likely to be a revolving stage for Japanese macaques. It is noteworthy that modes II and III show considerable associations in some sets of molecular and nonmolecular traits. In mode II, the deviations of peripheral populations found in morphological or reproductive characteristics show substantial correlation with those in nuclear genes, suggesting genetic control of those biological traits. The discontinuous differentiation recognized as mode III also suggests a tight association of ecological segregation, such as in habitat use and feeding ecology, with historical changes of geographical distribution inferred from mtDNA phylogeography.

For understanding the evolutionary adaptation to environments in Japanese macaques, it is important to further investigate the details of local differentiation patterns in various biological traits, and for their association with differentiation in genes or evolutionary changes in environmental conditions. The classification of associating characteristics and analysis on the causes of those associations seems to be the key for understanding evolution in Japanese macaques.

Comparative studies between Japanese macaques and other organisms on the same archipelago to determine similarities in patterns or common factors of local differentiations are of great interest. Such studies will give us insights into natural history and evolutionary mechanisms in Japan, and it is preferable to perform comparisons not only at the species level but also at the ecosystem level. It is inferable that the differentiation and history of Japanese macaques will correlate with the differentiation in floral, microorganismal, or entomological elements of the ecosystem that are sensitive to fluctuation of environments.

Advances in genome studies are powerful tools to support future population studies of Japanese macaques. The achievement of the draft screening of rhesus genome (Rhesus Macaque Genome Sequencing and Analysis Consortium 2007) is making an epoch in population genetic studies of macaques (Street et al. 2007; Satkoski et al. 2008). As we are able to apply new ideas and tools to population studies of Japanese macaques, then the species is expected to represent a pilot study for nonhuman primates.

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# Part II
# Intra-specific Variation: Ecology and Conservation

# Chapter 4: Ecological Adaptations of Temperate Primates: Population Density of Japanese Macaques

**Goro Hanya**

## 4.1 Habitat of Japanese Macaques

The importance of the ecology of Japanese macaques lies in the fact that they are typical "temperate primates." Temperate forest is a marginal habitat for primates, as the center of the primate distribution is tropical rainforest. If we define the border between temperate and tropical areas as the Tropics of Cancer and Capricorn, approximately 20 genera of eight families of primates are distributed in temperate areas, including East Asia (Japan and China), South Asia (Bhutan, Nepal, India, Afghanistan, Pakistan, and Bangladesh), South Africa, North Africa (Morocco and Algeria), Madagascar, and South America (Argentina). Among them, ten species are distributed more widely in temperate than in tropical regions, including five species of macaques (*Macaca fuscata*, *Macaca cyclopis*, *Macaca mulatta*, *Macaca thibetana*, and *Macaca sinica*), three species of golden monkeys (*Rhinopithecus bieti*, *Rhinopithecus roxellana*, and *Rhinopithecus brelichi*), and capped and golden langurs (*Trachypithecus pileatus* and *Trachypithecus geei*). Among them, five species (Japanese and Barbary macaques, Sichuan and Guizhou golden monkeys, and golden langurs) are distributed exclusively in temperate regions (Fleagle 1999). Japanese macaques are undoubtedly the best studied temperate primate species.

Japanese macaques are distributed widely in the Japanese archipelago, from Shimokita Peninsula in the north to Yakushima Island in the south, including Honshu, Shikoku, and Kyushu Islands and some nearby islands (Fig. 4.1). In the lowland forest of Yakushima, they live in subtropical evergreen broad-leaved forest, and the average monthly temperature rarely drops below 10°C. On the other hand, in Shiga Heights in Nagano Prefecture, the temperature drops below –20°C and the snow cover reaches as much as several meters (see Table I in Preface). Japanese macaques in northern Japan have morphological and physiological adaptations against cold,

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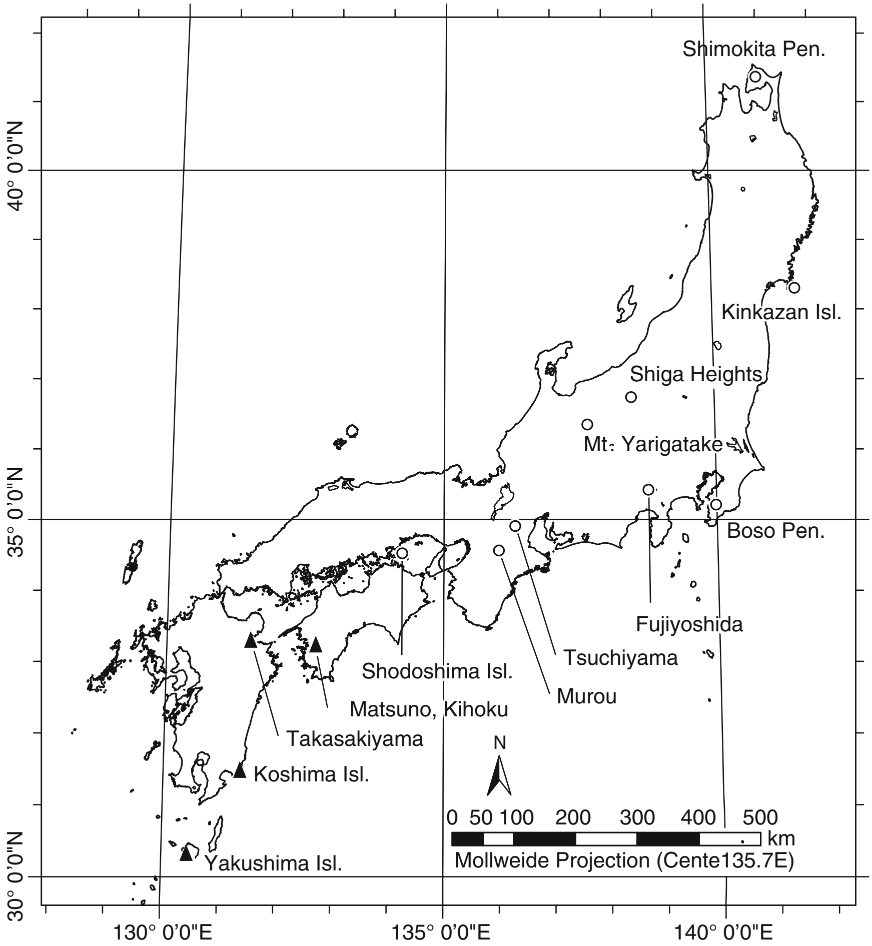

**Fig. 4.1** Study sites in this chapter. *Circles* indicate cool-temperate deciduous forests, and *triangles* indicate warm-temperate evergreen forests. (The base map is originated from "Boundary data of cities, towns and villages of Japan, ver. 6.2" by ESRI Japan Corporation, with permission)

such as increase of hair density (Hori et al. 1977; Inagaki and Hamada 1985; Tokura et al. 1975; for details, see Chap. 2). Considering that the origin of primates is in the tropics, the extensiveness of the ecological adaptation of this species is surprising.

The habitat of Japanese macaques is roughly categorized as warm-temperate evergreen forest in southwestern Japan and cool-temperate deciduous forest in northeastern Japan. The fundamental difference between the two habitats is whether trees drop their leaves in winter. Winter is the bottleneck season in temperate regions, which poses severe thermoregulatory cost and food deficiency. Difference in leaf food availability between the two habitats has a profound effect on the ecology of Japanese macaques.

In this chapter, I explore how Japanese macaques adapt to the two contrasting habitats, evergreen and deciduous forests, with special reference to population density. First, I outline the difference in the diet between the two habitats, as a background of the interhabitat difference in population density. Then, I explore the determinants of the population density and home range size per animal that is required to secure foods by comparison at two scales (entire Japan and within Yakushima). Then, as an extreme example of marginal habitat in temperate forests, I introduce the Japanese macaques living in high mountains (Mt. Yarigatake, 3,180 m a.s.l.). Finally, I discuss the ecology of Japanese macaques in disturbed habitats. Whether evergreen or deciduous forests, only a little of their "original" habitats (primary forest) remains for Japanese macaques. Most of the forested habitats have been converted into more or less artificial plantations of conifers or croplands. I describe how Japanese macaques adapt to these human-made habitats, in particular, the effects of logging on density and food availability.

## 4.2 Diet of Japanese Macaques

### *4.2.1 Regional Variations*

I compare the diet in three habitats, where Japanese macaques have been studied by direct observation for at least 1 year (Agetsuma and Nakagawa 1998; Hanya 2004a). The three study sites are Kinkazan Island (deciduous forest), the lowland of Yakushima (evergreen forest), and the highland coniferous forest of Yakushima (evergreen forest). In all three areas, Japanese macaques eat mature leaves, young leaves, fruits, seeds, flowers, and animal matter such as insects (Fig. 4.2). However, the importance of each food differs among sites. In the coniferous forest of Yakushima, the mature leaf is the most important food, which constitutes 38% of the annual feeding time (Fig. 4.3); however, fruit is the most important food in lowland Yakushima and seeds in Kinkazan. In the coniferous forest of Yakushima, the macaques spend a long time feeding on flowers and fungi, which are only minor foods in other areas. Bark is eaten for a long time only in Kinkazan. Japanese macaques are assumed to be frugivores (Bercovitch and Huffman 1999); however, Japanese macaques in the coniferous forest of Yakushima are not frugivores because fruit and seed feeding time is only 17% (Hanya 2004a). They spent 45% of their annual feeding time on fiber-rich foods, such as leaves, pith, and root (Hanya 2004a), which is close to the average of the 24 species of forestomach-fermenting folivorous colobines (52%; Kirkpatrick 1999). On the other hand, in the lowland of Yakushima, fruits and seeds are the most important foods for Japanese macaques (Hill 1997). Considering that lowland and coniferous forests of Yakushima are only 7 km apart each other, the diet of Japanese macaques is surprisingly flexible.

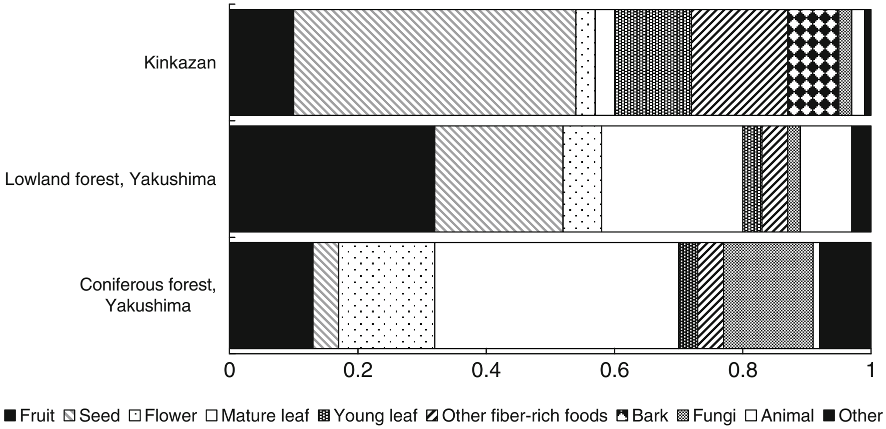

**Fig. 4.2** Annual diet of Japanese macaques in Kinkazan, lowland forest of Yakushima, and coniferous forest of Yakushima. Proportion to the annual feeding time is shown. Focal animal sampling in Kinkazan and coniferous forest of Yakushima; scan sampling in lowland forest of Yakushima. (Modified from Agetsuma and Nakagawa 1998 and Hanya 2004a)

**Fig. 4.3** A female Japanese macaque eats mature leaves of *Symplocos myrtacea* in coniferous forest of Yakushima

Patterns of seasonal changes are common among these three sites. The macaques eat young leaves in spring. In summer, they eat various foods such as fruits, mature leaves, fungi, seeds, and insects. In autumn, they eat fruits and seeds. In winter, after consuming the fruits and seeds produced in the preceding autumn, they eat mature leaves of evergreen trees in Yakushima (both lowland and coniferous forests) or bark and winter buds in the deciduous forest of Kinkazan. Even in the coniferous forest where the annul feeding time on fruits and seeds is short, macaques eat fruits and seeds whenever they are available (Hanya 2004a). Therefore, fruits and seeds are preferred foods. The reason that fruit and seed feeding time is short in the coniferous forest is because fruit production is less than in the lowland forest (about one-third; Hanya et al. 2003).

I can point out two important characteristics of the diet of this species. One is that they can survive with a low-quality fiber-rich diet. The other is that they prefer high-quality fruits and seeds and eat them whenever available. Both these strategies are useful adaptations in temperate regions, where fluctuations in fruit availability are intense, and sometimes no fruit is available for several months of the year (Thompson and Willson 1979; Herrera 1984). In these environments, they need to depend on low-quality foods when fruits are not available. At the same time, the preference for fruit is also useful in the temperate region because excess food intake can be saved as fat to help animals survive in winter (Wada 1975).

### *4.2.2 Cause of Food Deficiency in Winter*

In temperate regions, it is important to survive in winter, when the climate is harsh and food availability is low. Nakagawa et al. (1996) compared the degree of food deficiency in evergreen and deciduous habitats, where food conditions in winter differ. Nakagawa et al. (1996) distinguished two kinds of limitations that cause food deficiency in Japanese macaques. One is the limitation by gut capacity. When they feed on nutritionally low-quality foods, they cannot gain energy requirements even if they eat to their gut capacity. Empirically, it is known that the maximum daily intake of Japanese macaques is 300 g in dry weight (Iwamoto 1982). Therefore, if the energy content in 300 g of the food items is less than daily energy requirements, macaques cannot satisfy their energy requirements even if they eat to the limit of their guts, and thus they fall into energy deficiency. Most of the winter foods for Japanese macaques, such as mature leaves, bark, and buds, are those kinds of foods. The other limitation is time. Japanese macaques can spent only 70% of the daytime on feeding at maximum. Daylength is short in winter, so available time for feeding is about 7 h per day. Therefore, if the energy content of the foods that can be ingested in those 7 h is less than the daily energy requirement, macaques fall into food deficiency even if they spend most of their time on feeding. It is very time consuming to pick up small winter buds or strip and ingest the thin cambium on the inner side of bark until macaques can consume sufficient amounts. In fact, Japanese macaques in the deciduous forest in winter, where they depend on these time-consuming foods, spent 70% of the daytime on feeding.

Nakagawa et al. (1996) revealed that the reasons for food deficiency in winter for Japanese macaques differ between evergreen and deciduous forests. In the evergreen forest, they are limited by their gut capacity because the foods, such as mature leaves, are nutritionally of low quality. In the deciduous forest, in addition to the low-quality foods, they are limited by low feeding rates. As a result, food deficiency is more severe in deciduous forests. In evergreen forests, their energy intake is about 90% of the energy requirements. In contrast, in a deciduous forest, intake is only 60% of the requirements.

In both these habitats, energy intake during winter seems to be less than their energy requirements (Iwamoto 1982; Nakagawa 1989a; Nakayama et al. 1999; Tsuji et al. 2008). The macaques employ various behavioral tactics to survive winter; for example, they increase time spent feeding on abundant fallen fruits, which do not require much searching time (cost) (Nakagawa 1989b); they stop eating fruits that require much searching time (Agetsuma 1995); they shorten the time spent moving (Agetsuma and Nakagawa 1998; Hanya 2004b) and their daily travel distance (Nakagawa 1989b; Wada and Tokida 1981); and they save energy by behavioral thermoregulation, such as huddling and sunbathing (Hanya et al. 2007; Fig. 4.4). However, they cannot decrease their basal metabolism as do hibernating animals, so their energy budget becomes deficient. They eat high-quality fruits and seeds in autumn and accumulate them as fat. In winter, they survive by consuming the accumulated fat.

Muroyama et al. (2006) analyzed the fat accumulation of 197 fresh carcasses of Japanese macaques in Shimane and Chiba Prefectures, which were captured for pest control. The amount of accumulated fat was large in spring and autumn and small in summer and winter. According to the weekly body measurements of provisioned Japanese macaques in Takasakiyama (Kurita et al. 2002), body weight was greatest at the end of November and decreased gradually until the middle of February. Because food deficiency is more severe in deciduous than in evergreen forests,

**Fig. 4.4** In coniferous forest of Yakushima, Japanese macaques huddle together for a long time on cold winter days

the amount of fat accumulation is predicted to be larger in deciduous than in evergreen forests. In fact, the decrease of body weight is 10% in the deciduous forest of Shiga Heights (Wada 1975) but it is only 5% in the evergreen forest of Koshima (Mori 1979).

## 4.3 Variations in Home Range and Population Density

### *4.3.1 Comparison Between the Evergreen and Deciduous Forests*

Furuichi et al. (1982) studied the ranging pattern of three groups of Japanese macaques of Shimokita in winter. These groups selectively utilized deciduous forest and conifer (*Thujopsis dolabrata*)/deciduous mixed forests and passed through cedar plantations. The area of deciduous plus mixed forest divided by the group size, that is, per-animal "essential resource area" (Furuichi et al. 1982), was constant among the three groups. This observation indicates the very simple rule that the home range is proportional to group size. Takasaki (1981b) extended this comparison to the whole of Japan, including 32 groups.

Takasaki found that (1) when disturbed areas are excluded, home range and group size were proportional in evergreen and deciduous forests, respectively, and (2) home range size per animal was, on average, 2.0 ha in evergreen forests and 15.1 ha in deciduous forests (Fig. 4.5). Caution is needed because these relationships are only rough ones, after the log-transformation of both group size and home range size. In fact, home range size per animal was variable within each forest type. However, one

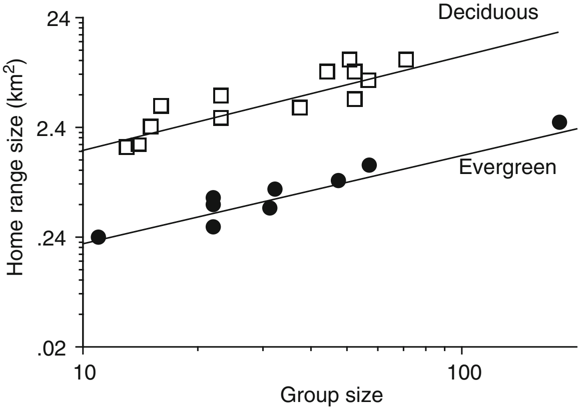

**Fig. 4.5** Relationships between group size and home range size in Japanese macaques. Note that both axes are log scale. (Modified from Takasaki 1981b)

**Table 4.1** Variations in population density of Japanese macaques

| Population | Habitat | Latitude | Density (animals/km$^2$) |
|---|---|---|---|
| Yakushima, 0–300 m a.s.l. | Evergreen | 30 | 62–100 |
| Koshima | Evergreen | 31 | 71 |
| Takasakiyama | Evergreen | 33 | 67 |
| Kawaradake | Evergreen | 34 | 59 |
| Yakushima, 900–1,300 m a.s.l. | Evergreen | 30 | 36 |
| Toimisaki | Evergreen | 31 | 33 |
| Yakushima, 300–900 m a.s.l. | Evergreen | 30 | 30–36 |
| Kinkazan | Deciduous | 38 | 18–27 |
| Shodoshima | Deciduous | 34 | 12.7–13.8 |
| Shimokita | Deciduous | 41 | 8.2 |
| Shiga Heights | Deciduous | 37 | 4–5.6 |

*Source:* Cited from Hanya et al. (2006)

can point out that a clear-cut difference in home range size per animal between evergreen and deciduous forests can be suggested even with this rough analysis.

Home range size per animal is the inverse of population density if the overlap of home range between different groups is negligible. We compiled data in Takasaki (1981b) and those studies published after the 1980s to analyze regional variations in population density (Table 4.1). Population density in evergreen forests was consistently higher than in deciduous forests (Hanya et al. 2006). However, there was no discrete difference, such as for home range size per animal. The population density in Kinkazan, which is highest among deciduous forests, is not so different from that in Toimisaki, which is smallest among evergreen forests.

### 4.3.2 *Cause of the Difference Between Evergreen and Deciduous Forests*

Why does the home range per animal or population density differ between evergreen and deciduous forests? As I have reviewed, there is a difference in food conditions in winter, but other possibilities also need to be examined.

First, primary production, thus the total food abundance, may be different between the two forest types. According to a survey of 170 Japanese forests, litterfall (which is correlated with primary production) is 3.88 t/ha/year in evergreen forest and 3.27 t/ha/year in deciduous forest, respectively, on average (Saito 1981). It is evident that the difference in total food abundance is not so much as eightfold, as is true in home range size per animal. Second, the severity of coldness in winter, or thermoregulatory cost, might be relevant. Roughly speaking, deciduous forests in northeastern Japan are cooler than evergreen forests in southeastern Japan. If the difference in temperature directly affects home range size and density, there must be a latitudinal continuous cline in population density and home range size per animal. Practically, it is difficult to judge whether the observed pattern is a north–south cline, or a deciduous–evergreen zonal gap, and the real picture is probably a mixture of these two effects. However, in two central Japanese sites (Shodoshima Island and Boso Peninsula), where the potential natural vegetation is evergreen but the actual (secondary) vegetation is deciduous, home range size per animal is close to those in the deciduous forest in northern Japan (Takasaki 1981a). Therefore, it is safe to conclude that a discrete difference between the two forest types surely exists.

The foregoing discussion strongly suggests that difference in food conditions in winter is the most likely cause of the regional variations in density and home range size per animal. Seasonal variation in home range size is a key factor to explore this issue. When the home range size varies with season, it is the season in which home range becomes the largest that determines the annual home range and thus population density. Japanese macaques eat high-quality fruits and seeds in autumn and accumulate fat to survive food deficiency in winter. If the food conditions in winter affect the annual home range size, annual home range size is determined by the area that is required to secure enough foods for fat accumulation. We reviewed seasonal variations in home range size of 11 groups in eight areas of Japan, from Yakushima to Shimokita. In most groups, the home range was largest in summer or autumn and smallest in spring or winter (Table 4.2; Hanya et al. 2006). Therefore, home range size in summer and autumn affects the annual home range and thus population density. The amounts of their main foods in these seasons, such as fruits and seeds, are limited, so macaques need to range over a wide area to secure foods to accumulate enough fat. In contrast, in winter, the main foods, such as mature leaves, buds, and bark, are abundant, so they do not need to range over a large area. Animals without fat accumulation abilities need to search for high-quality foods even in lean seasons, so they would need to range the

**Table 4.2** Seasonal changes in home range size of Japanese macaques

| Area/group | Habitat | Latitude | Spring | Summer | Autumn | Winter |
|---|---|---|---|---|---|---|
| Yakushima, coniferous forest | Evergreen | 30 | 1.06 | (0.89)[a] | **1.81** | 1.05 |
| Yakushima, coastal forest | Evergreen | 30 | 0.29 | 0.3 | **0.58** | 0.37 |
| Matuno, IS group | Evergreen | 33 | 7.19 | 6.36 | **8.39** | 3.01 |
| Kihoku, NK group | Evergreen | 33 | 7.64 | 12.0 | 3.36 | **13.2** |
| Tsuchiyama, Ni group | Deciduous | 35 | 5.02 | 6.83 | **9.70** | 2.97 |
| Tsuchiyama, Ke group | Deciduous | 35 | 9.35 | 10.7 | **21.6** | 12.5 |
| Murou | Deciduous | 35 | 22.8 | **39.7** | 35.2 | 4.02 |
| Fujiyoshida, YS group | Deciduous | 35 | 3.92 | **7.83** | 6.72 | 6.55 |
| Fujiyoshida, NK group | Deciduous | 35 | 5.48 | **11.8** | 10.4 | 5.25 |
| Shiga Heights | Deciduous | 37 | **3.92** | 2.29 | 3.22 | 1.65 |
| Shimokita | Deciduous | 41 | 8.6 | **21.6** | 16.7 | 19 |

Maximum home range sizes are in *bold*; minimum sizes are *underlined*

[a] Parenthesized home range size was based on data less than the required quantity (>15 all-day ranges)

*Source:* Cited from Hanya et al. (2006)

largest area in the lean season. Japanese macaques range a small area in the lean season (winter) because they have the ability to accumulate fat.

### *4.3.3 Variation Within Evergreen Forest: A Case in Yakushima*

I showed in Table 4.1 that population density varies even in the same forest types. For example, among deciduous forests, population density is higher in Kinkazan and Shodoshima with little snowfall than in snowy Shiga Heights and Shimokita. This difference may be explained by the difference in food availability in winter, especially herbs and fallen seeds on the ground, which cannot be found and eaten when there is snow cover (Nakagawa 1989a). On the other hand, density varies considerably at a much smaller scale, for example, in Yakushima. The lowland of Yakushima is covered with warm-temperate evergreen forest. The highland of Yakushima is covered with a mixed forest of conifers and evergreen broad-leaved trees. Therefore, with respect to leaf availability in winter, there is no variation within Yakushima. However, the variation in population density becomes as great as threefold (Yoshihiro et al. 1999). Data are still lacking for home range size in the highland; however, one group with fewer than 30 individuals had a home range of 2.7 $km^2$. In the lowland, groups of similar size have home ranges of about 1 $km^2$. Variation in home range size per animal is probably as great as that of population density.

To explore the habitat characteristics that affect altitudinal variations in density, we set three vegetation plots (50 m × 50 m) at 280, 600, and 1,100 m a.s.l. According to the 3-year observation, total annual fruit abundance was highest in the lowland, and there was no difference between the mid- and high-altitude forests (Fig. 4.6b). This pattern is the same as that of macaque population density: population density was high only below 400 m a.s.l. and did not differ among the higher zones (Fig. 4.6a). On the other hand, the number of months when fruit is available decreased gradually with altitude (Fig. 4.6c). Based on these data, we concluded that total annual fruit abundance, not the seasonal pattern of fruit production, affects the altitudinal variations of the density of Japanese macaques in Yakushima (Hanya et al. 2004).

### *4.3.4 Determinants of Population Density: A Synthesis*

Comparisons at two scales, that is, the whole of Japan and within Yakushima, suggest the following mechanism for the determination of population density. Under constant total annual fruit abundance, population density is lower with more severe winter food conditions, because macaques need to range over a larger area to secure more foods in autumn for fat accumulation. On the other hand, under the same food conditions in winter, when there is greatest total annual fruit abundance, macaques need to range over only a smaller area to secure foods in autumn

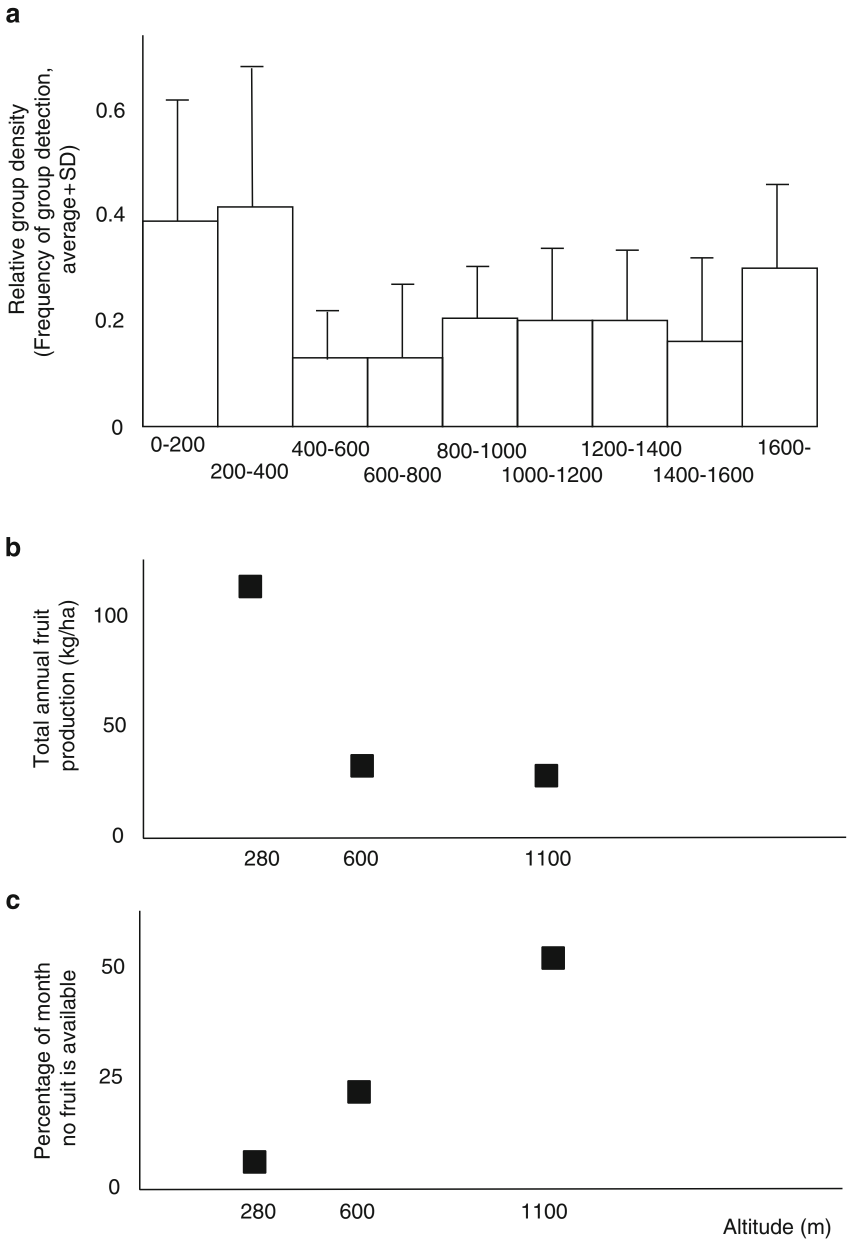

**Fig. 4.6** Altitudinal variation of group density of Japanese macaques (**a**), total annual fruit production (**b**), and the proportion of the time that no fruits are available during 1 year in Yakushima (**c**). (Modified from Hanya et al. 2004)

for fat accumulation, and thus their density becomes higher. The combination of total annual food abundance and food conditions in lean periods determines the population density and/or home range size per animal, and the key factor that links these two parameters is fat accumulation, which is an essential adaptation in temperate forests.

Interestingly, the same kinds of mechanism seem to work in the population density of other mammals. The essential mechanism of fat accumulation from the ecological point of view is to store foods for future consumption (Jönsson 1997). Fat-accumulating animals save foods inside their bodies, but the function in the ecological sense is the same when animals save foods outside their body. Scatter-hoarding by rodents is another example of such saving outside of the body. The importance of scatter-hoarding in density can be seen in the population regulation of frugivorous rodents in Barro Colorado Island (Smythe et al. 1982). During bottleneck periods, pacas (*Agouti paca*) relied on leaves, while agoutis (*Dasyprocta punctata*) ate scatter-hoarded seeds. The effect of poor fruiting on density was more severe for agoutis. The content of the data differs between Japanese macaques and agoutis (temporal fluctuations for agouti and regional variations in Japanese macaques); however, both examples indicate that density of animals having the ability to save foods is limited by the total abundance of high-quality foods. The density of animals that lack this ability, such as pacas, is not affected by the decrease of high-quality foods.

## 4.4 Japanese Macaques in Alpine Grasslands

The highest elevation that Japanese macaques are known to use is 3,180 m a.s.l., which is Mt. Yarigatake in central Japan (Izumiyama 2002). The group using the summit has a home range in the deciduous broad-leaved forest in the upper Takase River in winter around 1,700 m a.s.l. From May to June, they move upward to cross the subalpine coniferous forest and reach the alpine grasslands near the summit, above 3,000 m a.s.l. (for a photograph, see Fig. 3.9). Home range from February to May, when they use the broad-leaved forest, was 3.9 km$^2$, and it was 14.4 km$^2$ from July to September when they use alpine grasslands. In winter, this group fed on bark and winter buds of deciduous broad-leaved trees, such as *Hydrangea paniculata*, *Acanthopanax sciadophylloides*, and *Rhus trichocarpa*. In summer, they fed on grasses such as *Angelica pubescens*, *Coelopleurum multisectum*, and *Cirsium* spp. or seeds of dwarf pine *Pinus pumila*. Izumiyama (2002) explains that Japanese macaques move upward to track the young leaf flushing from low altitude to high altitude. The mid-altitude subalpine coniferous forest is poor in foods for Japanese macaques and too narrow a zone; thus, macaques pass through it and reach the alpine grasslands.

Yakushima macaques also live above the forest limit. In Yakushima, the border between the coniferous forest and subalpine grasslands of bamboo (*Pseudosasa owatarii*) is 1,600 m a.s.l. One group of Japanese macaques appears at the summit of the second highest peak of Yakushima, Mt. Nagata (1,886 m a.s.l.) in summer (Hanya et al. 2004). They eat mainly leaves of bamboo. In winter, there are no Japanese macaques around Mt. Nagata, and the upper limit of their distribution drops to 1,450 m (Yoshihiro 1995). The north of the Mt. Nagata is a steep cliff, and the summit is close to the forest edge. According to our 4-day census, the macaques always appear at the summit by climbing up the cliff (Hanya 2002). This habit is different from the group using the summit of Mt. Yarigatake in central Japan (Izumiyama 2002), which stays completely out of the forest in summer. In fact, Mt. Miyanoura (1,936 m a.s.l.), the highest summit in Yakushima, is extensively surrounded by grasslands and no macaque group is distributed there (Yoshihiro 1995). The elevation of Mt. Miyanoura is similar to that of Mt. Nagata, so the reason that macaques are not distributed in Mt. Miyanoura is not because of the difference in vegetation but because there are no forests around it that can be used as a foothold.

## 4.5 Effects of Logging

So far, I have discussed mainly populations with minimum human disturbance. However, the Japanese forest has been changed considerably since the 1960s and 1970s by “expansive afforestation,” namely, deforestation of broad-leaved trees and afforestation with conifers, such as Japanese cedar *Cryptomeria japonica* and hinoki cypress *Chamaecyparis obtusa*. As a result, 41% of Japanese forests has been converted to artificial coniferous forests (Forest Agency, Japan 2007). Most of the populations of Japanese macaques live under the strong influence of human economic activities, such as logging and agriculture (for details, see Chap. 7 and Topic 4). In the previous sections of this chapter, I have discussed populations such as those in Yakushima and Kinkazan, where natural vegetation remains over an exceptionally wide area or data were collected several decades ago, when expansive afforestation had not taken place. To understand the present-day Japanese macaques, their lives in human-made habitats, in particular in conifer plantations, need to be clarified.

We compared the density and food availability of Japanese macaques in the coniferous forest of Yakushima with different logging and regeneration systems (Hanya et al. 2005). The study area included both primary forest protected as National Park and disturbed forest outside the park. At the time of the study (2000–2003), it had been 7–27 years since logging occurred. The regeneration system changed in 1984. Before 1984, expansive afforestation was conducted: forest was clear cut, the areas of felling were cleared, and 1,000–2,000 conifer saplings (*C. japonica*) of about 60 cm height were planted per hectare. Weeding was conducted once a year for a few years after logging. After 1984, no afforestation has occurred, and clear-cut forests have been left to regenerate with minimum human management. We refer to the former stands as “plantations” and the latter as “naturally regenerated.” The group density of Japanese macaques was highest in

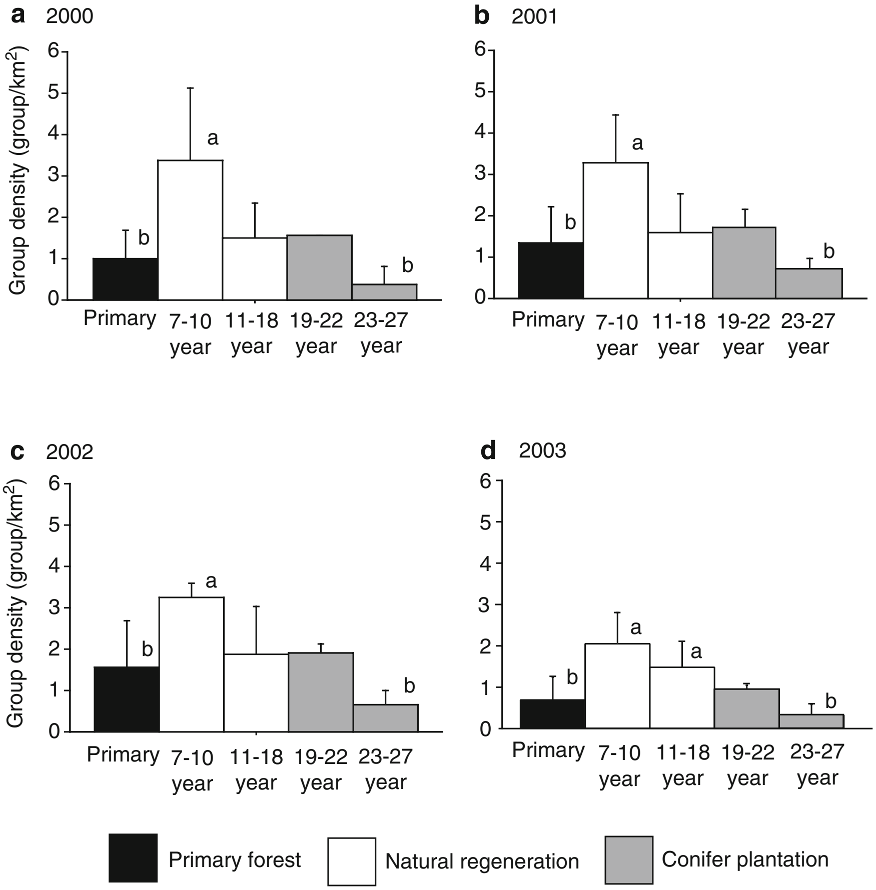

**Fig. 4.7** Variations in group density with respect to logging systems. *Alphabetical characters* indicate that a is significantly larger than b. (Modified from Hanya et al. 2005)

the naturally regenerated forest, intermediate in primary forest, and lowest in plantations (Fig. 4.7). Difference in food availability was similar to that of density (Fig. 4.8). Production of fruits that are eaten by macaques in naturally regenerated forests was ten times greater than that in primary forest. In conifer plantations, no food fruit was produced, because the vegetation was composed only of Japanese cedar.

In naturally regenerated forest, group density was higher than in primary forest, in accordance with the difference in fruit availability. In this forest, small trees such as *Symplocos tanakae*, *Eurya japonica*, and *Symplocos myrtacea* bear food fruits, but dominant trees in the canopy such as *C. japonica*, *Abies firma*, *Tsuga sieboldii*, *Trochodendron aralioides*, and *Stewartia monadelpha* do not provide foods for macaques. When tall trees are cut, small trees can receive more sunlight, which enhances their reproduction (Appanah and Manaf 1990; Guariguata and

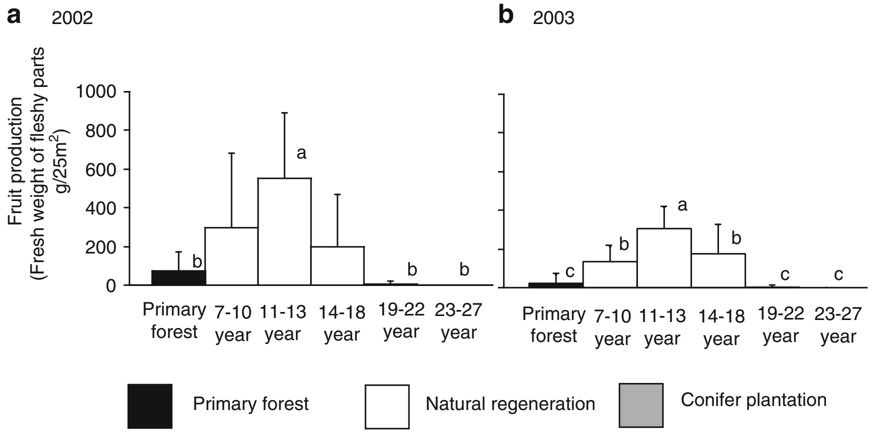

**Fig. 4.8** Variations in fruit availability with respect to logging systems. Fruit production in conifer plantation is negligible. *Alphabetical characters* indicate that a is significantly larger than b and a and b is significantly larger than c. (Modified from Hanya et al. 2005)

Saenz 2002). When such small trees offer a considerable amount of fruit food, the food availability for frugivores is increased by logging. In contrast, when large trees are the main sources of fruit foods for the frugivores, their density and fruit availability are known to be decreased by logging (Heydon and Bulloh 1997; Felton et al. 2003).

On the other hand, density was low in conifer plantations, which is explained by the low food availability there. Japanese macaques eat flowers of Japanese cedar (Hanya 2004a), so the food availability in conifer plantations is not zero. However, they need various kinds of foods for survival, in particular, high-quality fruits and seeds that satisfy their nutritional requirements. Therefore, a forest composed of Japanese cedar only has almost no food resource value.

In areas of very high proportion of conifer plantations, macaque home range becomes extremely large. A group in Shinshiro City, Aichi Prefecture had a home range of 47.3 km$^2$ (Aichi Prefecture 1994). In this area, 73% of the forest is conifer plantations. Based on the home range–group size relationships of Takasaki (1981b), a home range of the same group size (48) would be only 7.2 km$^2$ in deciduous forest without conifer plantations. These macaques probably use the fragmented broad-leaved forest and only pass through the conifer plantations, as the Shimokita groups did (Furuichi et al. 1982).

Our data on the effects of logging are in agreement with the scenario proposed by Agetsuma (2007), who considered that expansive afforestation caused crop-raiding by Japanese large mammals, including macaques. Food availability does not decrease immediately after logging. The availability of foods such as herbs or leaves and fruits of small trees may even increase. However, when 10 years or more have passed after the plantation of conifers, the planted conifers grow up and food availability decreases. Animals fall into food deficiency and begin to raid crops.

Agetsuma's scenario well explains the time lag between the expansive afforestation and start of crop-raiding by wildlife. In many places in Japan, expansive afforestation was conducted mainly in the 1960s and 1970s, and crop-raiding became a serious problem in the 1980s. Our data support Agetsuma's scenario on crop-raiding by Japanese macaques (see Chap. 7).

## 4.6 Future Scope

I have reviewed the adaptation of Japanese macaques to various types of vegetation, with special reference to their population density and home range size. They can live in very harsh habitats, such as alpine grasslands and snowy areas. They also live in forests that are composed mainly of conifer plantations. Enlarging home range (and decreasing population density) seems a common response for these difficult conditions. A home range of 47.3 $km^2$ may be one of the largest among primates. For example, a group of savanna-dwelling chimpanzees in Mt. Assirik, Senegal, is estimated to have a home range of approximately 72.1 $km^2$, which authors consider the largest size for nonhuman primates (Baldwin et al. 1981). As a result, the variation in population density reaches almost 100 fold. The maximum is in the lowland forest of Yakushima, 60–100 individuals/$km^2$ (Yoshihiro et al. 1999), and the minimum is Shinshiro City, 1 individual/$km^2$ (Aichi Prefecture 1994).

The large variation of population density of Japanese macaques is explained by food conditions in winter and the abundance of high-quality foods before winter arrives. The reason that these two factors affect density in combination is because Japanese macaques have ability to store foods by fat accumulation. Fat accumulation is a common physiological strategy for temperate and arctic endotherms (Thomas 1987), so the same mechanism may work for population density of other temperate animals. However, the level of food deficiency at which energy intake becomes a deficit differs from species to species. For example, macaques and golden monkeys live sympatrically in temperate areas of China, but the energy budget of the two species may differ, because macaques are caeco-colic-fermenters and golden monkeys are forestomach-fermenters (Lambert 1998). Because forestomach-fermenters can better digest fiber-rich foods (Lambert 1998), food deficiency in winter may be less severe for golden monkeys than for macaques.

There is sporadic evidence that some tropical primates also accumulate fat, or change their body weight seasonally (Uehara and Nishida 1987; Goldizen et al. 1988; Knott 1998; Atsalis 1999). For example, wild orangutans discharge urine containing ketones, which indicates the decomposition of fat. Orangutans accumulate fat during the mast-fruiting season and consume the accumulated fat during the postfruiting lean season (Knott 1998). However, it is not clear how widespread fat accumulation is among tropical primates. In the tropics, dependence on fat accumulation may be a risky strategy because the seasonal pattern of food availability cannot be simply predicted and thus it is difficult to ascertain how much fat accumulation is required for primates to survive the lean period.

Most of the studies on the determinants of density among frugivorous primates remain comparisons between different habitats or the examination of factors that affect density only indirectly, such as rainfall (Chapman and Balcomb 1998). Quantitative assessment of habitat parameters is rare, such as one of the Yakushima studies (Hanya et al. 2004). Stevenson (2001) provides one of the few examples, which indicated that fruit production (estimated by fruit fall) explained the biomass of 13 neotropical primate communities. However, Stevenson (2001) did not examine factors of total annual abundance and seasonality simultaneously, so it was not clear whether the same kind of mechanism works for neotropical primates as for Japanese macaques.

Examination of the seasonal variations in home range size and its relationship with food availability, as we did for Japanese macaques, may be useful to identify the season that limits animal populations. If the home range becomes largest during the lean period, food availability during the lean period can act as a bottleneck season that directly determines animal density. If the home range becomes the largest when food is abundant, total annual food abundance is a likely factor determining density. If we can examine the ability to accumulate fat and seasonal variations in food quality, based on knowledge of the digestive physiology of the species, we may find a general tendency of relationship between food (total annual food abundance and its seasonality) and animal density. So far, Japanese macaques offer the best example for the relationships between these aspects.

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# Chapter 5: Regional, Temporal, and Interindividual Variation in the Feeding Ecology of Japanese Macaques

**Yamato Tsuji**

## 5.1 Introduction

### *5.1.1 Feeding Ecology of Primates: A General View*

The feeding ecology of primate species often reflects their foraging behavior, as primates are faced with decisions about what, when, and where to feed (Oates 1987). The feeding behaviors in turn affect their feeding success, which ultimately influences population parameters such as mortality and birth rate. Thus, primate research must consider factors affecting variation in feeding ecology to better understand population dynamics (e.g., Dunber 1987; Cheney et al. 1988; Clutton-Brock and Pemberton 2004), to appropriately test socioecological theory (e.g., Nakagawa 1998, see also Chap. 12), and to apply the knowledge to primate pest management (Naughton-Treves et al. 1998; Yamada and Muroyama 2010, see also Chap. 7).

The feeding ecology of primate species is strongly affected by both food resource characteristics such as availability and distribution (Chivers 1977; Wrangham 1977; Oates 1987) and climate conditions such as air temperature, rainfall, and snowfall (Raemaekers 1980; Hill 2005; Cui et al. 2006). Because the intensity of these factors changes temporally, the feeding ecology of primates exhibits concomitant temporal dynamics. For group-living animals, on the other hand, a single group contains individuals of different social status (age and sex) whose nutritional demands also differ (van Schaik and van Noordwijk 1986; Kleiber 1987). In addition, dominance relationships exist among individuals (Kawamura 1958; Whitten 1983). I define these aspects of the primate group as "intrinsic factors," and the feeding ecology mirrors the interindividual variation within a single group (Clutton-Brock 1977).

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### 5.1.2 *Japanese Macaques and Their Habitat*

Not all nonhuman primates live in tropical regions, and several species inhabit temperate regions (Strier 2000; see also Chap. 4). In general, the degree of seasonal change in the food environment and climate conditions is greater in temperate than in tropical regions (Townsend et al. 2003), and the magnitude of yearly change in the food environment is just as high in the temperate regions as it is in the tropical regions (Herrera 1998). Thus, knowing the temporal variations in the temporal regions is a key to understanding the feeding ecology of the primates living there.

Japanese macaques (*Macaca fuscata*) are endemic to Japan and exhibit the northernmost distribution (30°21′–41°08′N) among extant nonhuman primates (Oi 2002). They are group living, and a group consists of different-aged individuals of both sexes. The potential natural vegetation of Japan is roughly classified into four types: cool-temperate deciduous broad-leaved forests in the northern parts, warm-temperate evergreen broad-leaved forests in the southern parts, subalpine evergreen coniferous forest, and alpine grassland (Fig. 5.1a). A unique characteristic of the climate in Japan is its clear seasonal changes in air temperature and rainfall

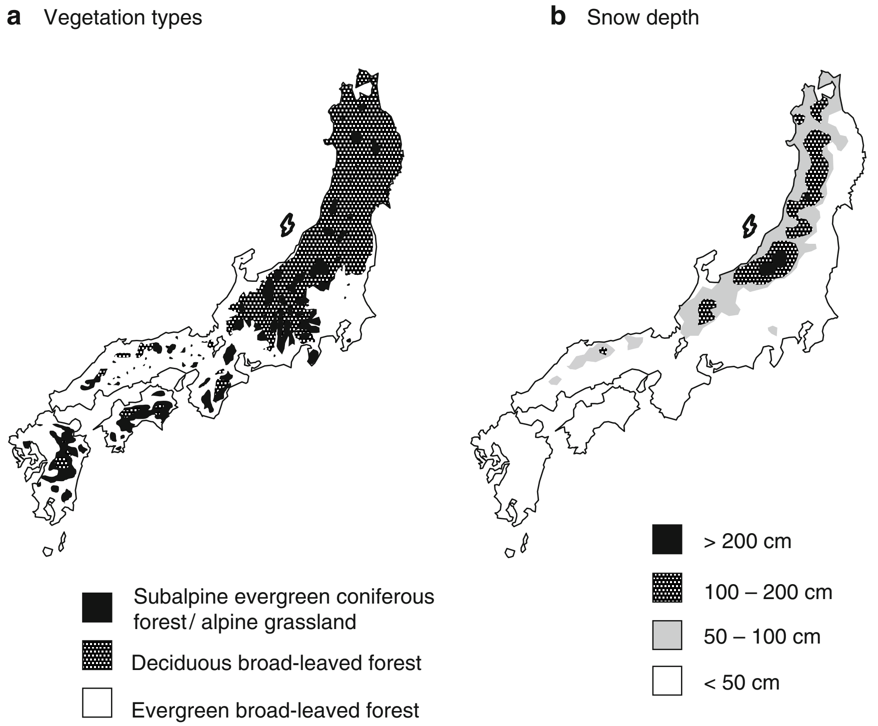

**Fig. 5.1** Distribution of potential natural vegetation (Horikawa 1968, cited in Uehara 1977) (**a**) and annual maximum depth of snow cover (average for the period 1971–2000) in Japan (Japan Meteorological Agency 1971–2000) (**b**)

(Fig. 5.2), and the year can be roughly divided into four seasons: spring (March to May), summer (June to August), autumn (September to November), and winter (December to February). In northern Japan, annual maximum depths of snow cover sometimes reach more than 2 m (Fig. 5.1b). In addition, yearly changes naturally occur in the amount of both fruiting (Komiyama et al. 1991; Noma 1996; Suzuki et al. 2005) and snowfall (Watanuki and Nakayama 1993). In turn, such fluctuations in food environment and climate conditions cause variations in the feeding ecology of Japanese macaques.

The dawn of Japanese primatology, mainly initiated by the Kyoto school, saw the first reports regarding the feeding ecology of Japanese macaques (Itani and Tokuda 1954). The progress of the research slowed during the 1960s and 1970s because the main interest of Japanese primatology shifted to the social system and cultural behavior of provisioned Japanese macaques (Kawai 1981,

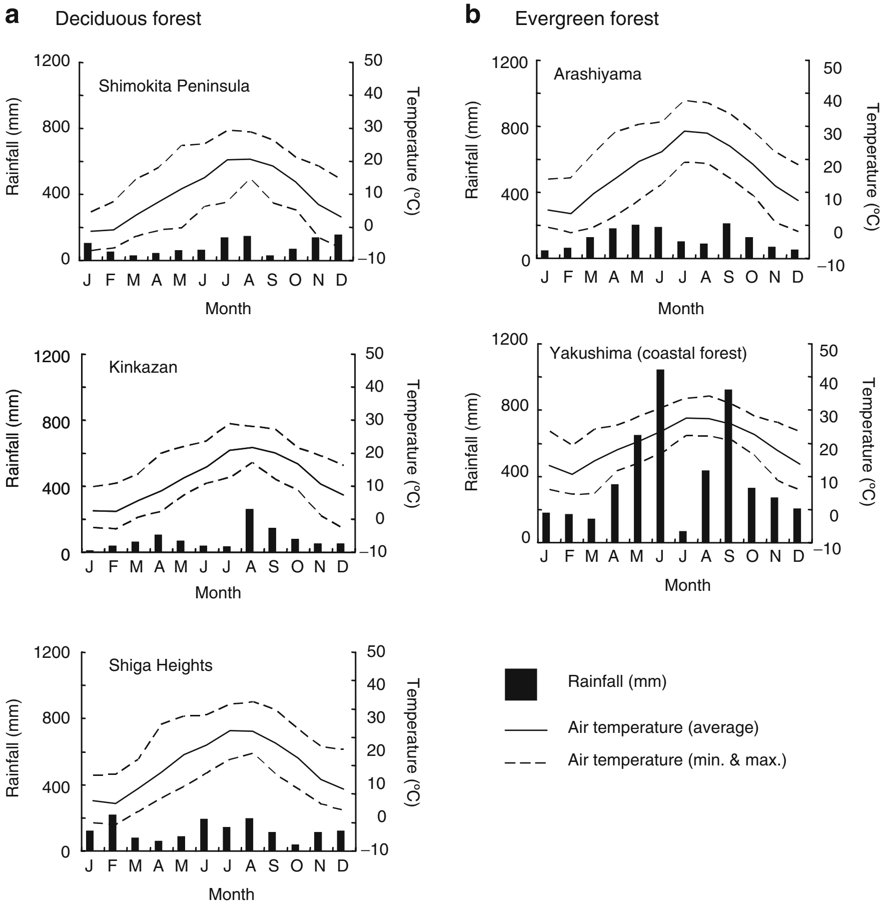

**Fig. 5.2** Seasonal changes in air temperature (*solid lines*, mean temperature; *dashed lines*, maximum and minimum temperature) and rainfall (*filled bars*) at five study sites [three sites in deciduous forests (**a**) and two in evergreen forests (**b**) (Japan Meteorological Agency 1971–2000)]

see also Chap. 1). Studies of the feeding ecology of wild Japanese macaques were revived in the early 1980s by young researchers (e.g., Maruhashi 1980; Ikeda 1982), and currently a great many data have been collected from various regions throughout Japan (Fig. 5.3).

In this chapter, I review variations in the feeding ecology of Japanese macaques, with special reference to regional, temporal (seasonal and yearly), and interindividual variations in the three main elements of feeding ecology: food habits, ranging behavior, and activity budgets. I also point out important effects of these variations, such as the food environment, climate conditions, and intrinsic factors.

The three main elements of feeding ecology (food habits, ranging, and activity) are interrelated: food habits affect both ranging patterns and time spent feeding or

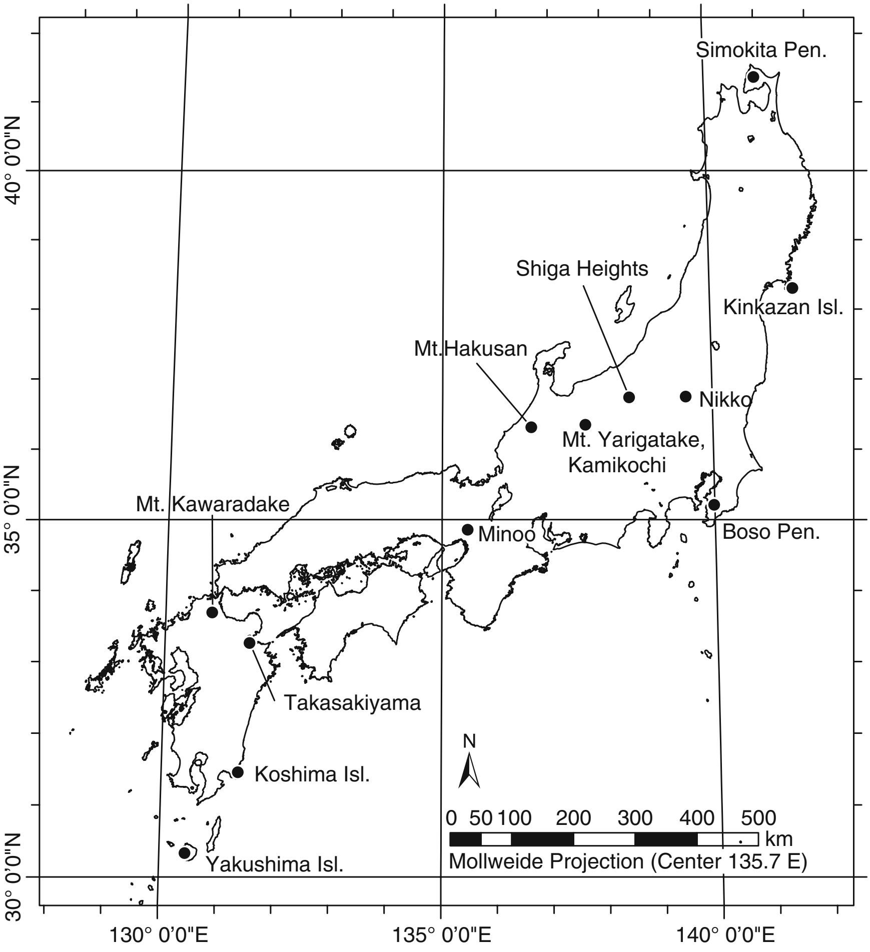

**Fig. 5.3** Japanese macaque study sites introduced in this chapter. The base map is originated from "Boundary data of cities, towns and villages of Japan ver. 6.2" by ESRI Japan Corporation (with permission)

moving, the latter of which consequently affects time spent resting (Agetsuma and Nakagawa 1998), and, ideally, these factors should be considered together. However, to facilitate the discussion of these topics, I introduce studies about each one separately. I close this chapter with an examination of future challenges to the study of the feeding ecology of Japanese macaques.

## 5.2 Food Habits

Japanese macaques feed on various parts of plants such as leaves, flowers, fruits, buds, and bark (reviewed by Suzuki 1965; Uehara 1975). They also feed on fungi, seaweed, animal materials (both vertebrates such as fish and reptiles, and invertebrates such as insects, spiders, and shellfish), and soil. The number of food items consumed by a macaque can amount to dozens to hundreds and can differ among habitats (or depend on the length of the study). However, the number of plant species on which macaques feed typically comprises just a small portion of the available flora: 109 of 574 species (19.0%) at Kinkazan Island (Izawa 2009), 176 of 700 (25.1%) at Shiga Heights (Ichiki et al. 1983), and 76 of 231 (32.9%) in the coastal forest of Yakushima Island (Maruhashi 1980). Furthermore, the number of staple foods is quite limited, and the percentage of time spent feeding on the top ten food items was between 58 and 73% in Shimokita Peninsula (Nakayama 2002) and between 83% and 91% in the coastal forest of Yakushima (Maruhashi 1980; Domingo-Roura and Yamagiwa 1999).

This intensive utilization of a limited number of foods indicates a strong preference for them; however, the factors affecting this preference have rarely been examined, with the exception of mature leaves, for which tree density, condensed tannin content, the protein–neutral detergent fiber (NDF) ratio (Hanya et al. 2007), and toughness (Hill and Lucas 1996) have been reported as important.

### *5.2.1 Regional Variation in Food Habits*

Japanese macaques are greatly influenced by their food environment, and clear regional differences exist between those living in cool- and warm-temperate zones. Figure 5.4 presents the food habits of Japanese macaques at seven study sites. Macaques inhabiting the cool-temperate zone (Kinkazan, Nikko, and Shiga Heights) fed more often on bark and dormant buds in winter (Figs. 5.4a and 5.5), whereas macaques inhabiting the warm-temperate zone (Koshima Islet and the two sites on Yakushima) fed primarily on fruits, flowers, and leaves during winter (Fig. 5.4c). The habitat in Boso Peninsula, where the natural vegetation is evergreen but the secondary vegetation is deciduous, is intermediate between cool- and warm-temperate zone habitats (Fig. 5.4b). Interestingly, on Yakushima,

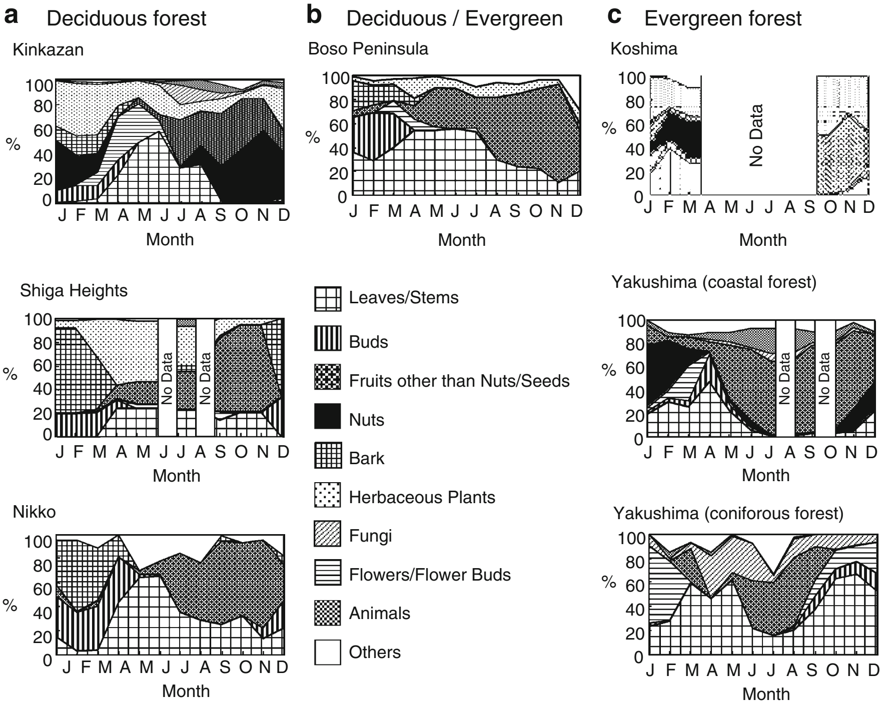

**Fig. 5.4** Food habits of Japanese macaques at seven study sites. *No data* indicates data were not available. (Kinkazan: Tsuji et al. 2006; Nikko: Koganezawa 1997; Shiga Heights: Suzuki 1965; Boso: Koganezawa 1975; Koshima: Iwamoto 1982; Yakushima (coastal forest): Agetsuma 1995a; Yakushima (coniferous forest): Hanya 2004a)

**Fig. 5.5** A female Japanese macaque feeds on dormant buds of *Swida macrophylla* in winter at Kinkzan Island

the food habits of macaques differed between the two altitude zones on the island: the group inhabiting the coastal forest (100 m a.s.l.) fed primarily on fruits (Agetsuma 1995a; Hill 1997), whereas the group inhabiting the coniferous forest (1,100 m a.s.l.) fed mainly on leaves (Hanya 2004a). This altitudinal variation in feeding habits can be attributed to differences in the amount of fruit production at the two altitudes (Hanya et al. 2003) and supports the proposition that the food habits of Japanese macaques are strongly affected by their food environment (for details, see also Chap. 4).

## *5.2.2 Temporal Variation in Food Habits*

### 5.2.2.1 Seasonal Changes

The food habits of Japanese macaques change seasonally and are also strongly influenced by their food environment (see Fig. 5.4). In the coniferous forest of Yakushima, for example, the amounts of fruits and seeds in the macaque diet followed seasonal changes in the availability of these resources (Hanya 2004a; Fig. 5.4). Agetsuma (1995a) and Hanya (2004a), on the other hand, found that seasonal changes in air temperature also significantly affected seasonal variation in food habits. For example, when the air temperature was low in the coniferous forest of Yakushima, the macaques fed more frequently on fiber-rich foods (bud, root, and pith) and herbs (Hanya 2004a). Agetsuma (2000) also experimentally demonstrated that the macaques preferred lower quality (represented by energy content per weight) food when the air temperature was low. However, several food items were eaten throughout the year regardless of the food environment and climate conditions: e.g., *Sasa nipponica* at Nikko (Koganezawa 1997) and *Symplocos myrtacea* in the coniferous forest of Yakushima (Hanya 2004a; see Fig. 5.4).

Together, these data lead to the question of whether seasonal variation in food habits affects the feeding success of Japanese macaques. After a pioneer study by Iwamoto (1974), several researchers have demonstrated seasonal changes in the nutritional condition of Japanese macaques (represented by energy and protein intake, or their balance). These studies combined behavioral observations and nutritional analyses of food items in both the cool-temperate (Shimokita: Nakayama et al. 1999; Kinkazan: Nakagawa 1989b, 1997; Tsuji et al. 2008) and warm-temperate zones (Koshima: Iwamoto 1982, 1997; Takasakiyama: Soumah and Yokota 1991). On Kinkazan, the nutritional condition of the macaques was highest in the autumn, followed by spring, and was the lowest in summer and winter (Fig. 5.6a). On the other hand, on Koshima, nutritional conditions were stable throughout the year except for August and September, when the macaques depended on provisioned foods (Fig. 5.6b). Nakagawa (1997) found that most of the energy and protein intake was explained by energy and protein intake rate, which was in turn affected by the rate of dry matter intake and crude protein content, respectively. Thus, a slow feeding rate in the winter was an important determinant of poor nutritional condition in the cool-temperate region (see also Nakagawa et al. 1996; Nakayama et al. 1999). In contrast, Nakagawa

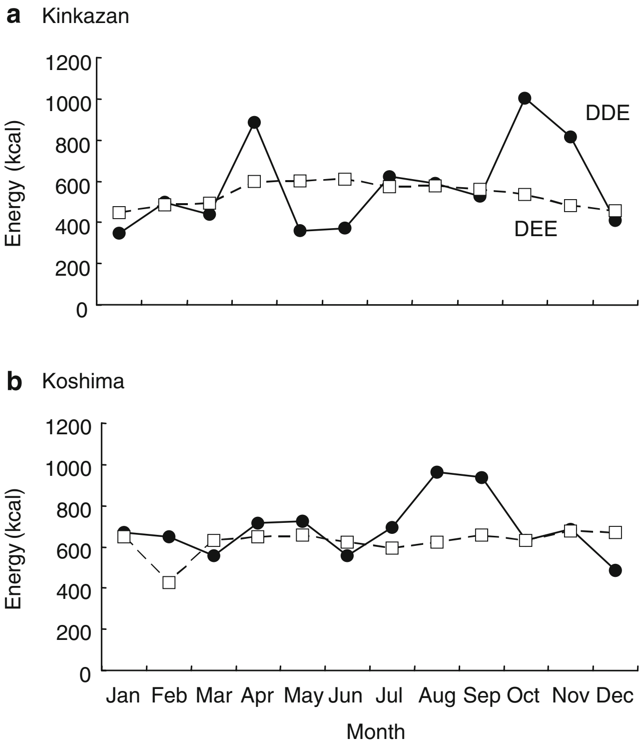

**Fig. 5.6** Monthly changes in average daily digestible energy intake (DDE, kcal day$^{-1}$) (*filled circles* and *solid line*) and daily energy expenditure (DEE, kcal day$^{-1}$) (*open squares* and *dashed line*) for Japanese macaques in Kinkazan (recalculated from Tsuji et al. 2008) (**a**) and Koshima (from Iwamoto 1997) (**b**)

et al. (1996) found that stomach bulk restriction (300 g dry weight maximum) was a more important determinant of poor nutritional condition in the warm-temperate region (for details, see Chap. 4).

### 5.2.2.2 Yearly Changes

The food habits of Japanese macaques also exhibit yearly changes that are affected by the food environment. Yearly changes in food habits have been reported both in cool-temperate (Shimokita: Watanuki and Nakayama 1993; Kinkazan: Tsuji et al. 2006) and warm-temperate zones (Yakushima: Hill and Agetsuma 1995). In particular, yearly variation in feeding on fruits (including berries and nuts) was remarkable. On Kinkazan, for example, large yearly variations in nut production (Fig. 5.7) caused

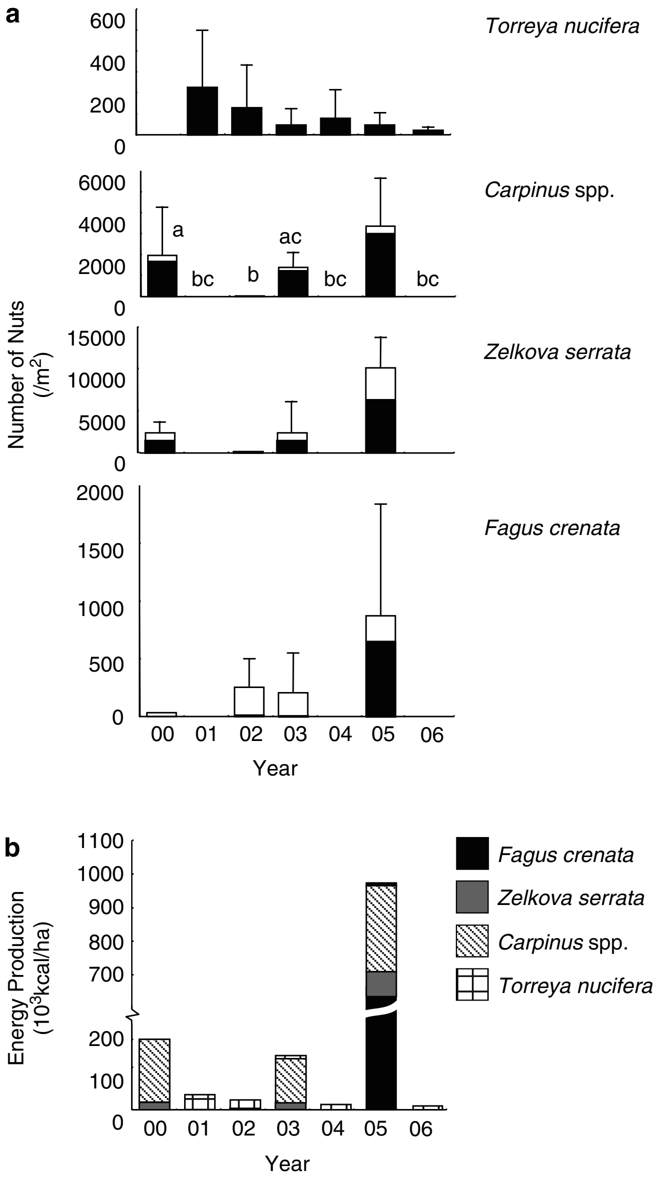

**Fig. 5.7** Yearly changes in nut density (m$^{-2}$) (**a**) and estimated energy production (**b**) from 2000–2001 to 2006–2007. *Letters above the bars* (a, b, c) indicate significant differences between bars with a different letter ($P < 0.05$). *Filled squares*, healthy nuts; *open squares*, empty nuts (including vacant and insect-damaged nuts). (From Tsuji 2007)

clear yearly changes in food habits (Fig. 5.8) (Tsuji et al. 2006). Because Japanese macaques overwinter by consuming body fat accumulated in the autumn (Nakagawa 1989b; Nakayama et al. 1999; Muroyama et al. 2006), yearly changes in autumn fruit production would affect not only their feeding success but also population parameters such as winter mortality and birth rate the next spring (Saito and Izawa 1997; Suzuki et al 1998; Izawa 2009).

Another factor affecting yearly changes in food habits is habitat deterioration caused by the macaques themselves. At Shiga Heights, for example, macaques changed their food habits after the death of *Acanthopanax sciadophylloies* trees as a consequence of repeated bark damage caused by macaque feeding (Wada 1983).

## *5.2.3 Interindividual Variation in Food Habits*

### 5.2.3.1 Effects of Age and Sex

Food habits vary among different age classes and between sexes (van Schaik and van Noordwijk 1986). This variation is likely caused by body size-specific nutritional requirements (Kleiber 1987) or sexual differences in foraging strategy (Schoener 1971). As a general rule, because of their high total nutrient requirements, low nutrient requirements per unit body weight, and the relatively low abundance of high-quality food, larger animals depend on abundant but low-quality food (the Jarman–Bell principle; Geist 1974). In Shimokita in winter, young Japanese macaques primarily fed on dormant buds, whereas adult macaques mainly fed on bark (Nakayama et al. 1999). On Yakushima, on the other hand, young macaques fed on insects (high-quality food but sparsely distributed), whereas adult macaques primarily fed on leaves (low-quality food but densely distributed) (Agetsuma 2001; Hanya 2003). In terms of sexual differences, male macaques on Yakushima fed more frequently on mature leaves compared to females (Agetsuma 2001). Given these data, the Jarman–Bell principle appears to be applicable to Japanese macaques. However, differences in the body size-specific physical abilities of macaques (e.g., lighter animals can more easily access dormant buds on thinner branches, and heavier animals cannot increase their feeding rate on dormant buds) may also contribute to differences in food habits among age classes (Nakayama et al. 1999; Agetsuma 2001). Female sexual proceptivity also affects food habits. Periovulatory female macaques in the coastal forest on Yakushima who copulated with multiple males spent less time feeding on insects than they did on anestrous days (Matsubara and Sprague 2004).

Nakayama et al. (1999) compared the degree of winter harshness among different age classes (juvenile and adults) by evaluating energy intake values. The thermoregulatory cost incurred by younger individuals in winter was estimated as lower because of smaller body size, indicating that winter was not as severe for younger macaques. In contrast, adult females did not satisfy their energy needs even if they used all the

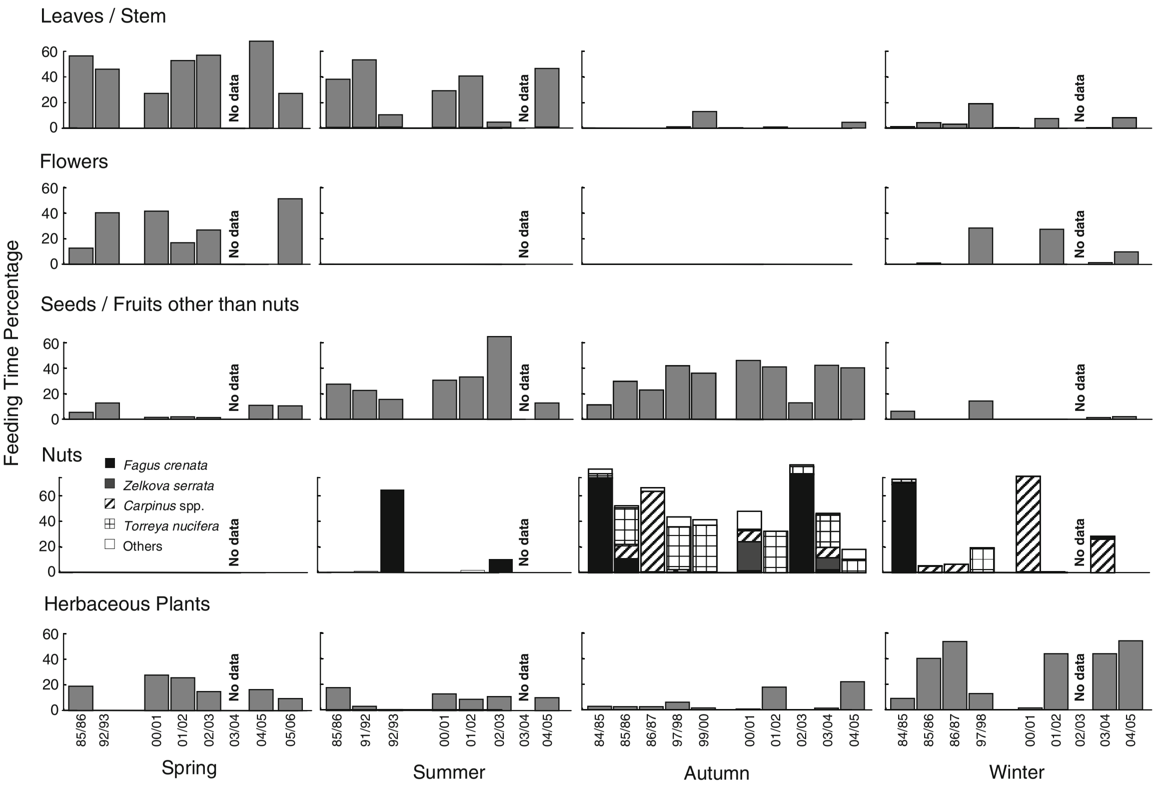

**Fig. 5.8** Yearly variation in the percentage of time spent feeding on the main foods in the diet of Japanese macaques on Kinkazan from October 1984 to May 2005. Spring, May and June; summer, July and August; autumn, September to November; winter, December to April. *No data* indicates a season or year for which data were not available. (From Tsuji et al. 2006)

body fat accumulated in autumn; therefore, winter appeared to be harsher for adult females (Nakayama et al. 1999). These findings imply that the food environment can require different feeding tactics for macaques belonging to individual age classes and sexes.

#### 5.2.3.2 Effects of Dominance Rank

Similar to other social animals, within-group contest competition (or interference) occurs among Japanese macaques when interindividual distances are too short (Furuichi 1983; Mori 1995). On Kinkazan, macaques ate together without contest competition when using large feeding patches or feeding patches at high densities (i.e., the interpatch distance was short). In contrast, contest competition occurred frequently when macaques used small feeding patches or feeding patches at low densities (i.e., interpatch distance was long), which, in turn, led to differences in the feeding success among different dominance ranks (Saito 1996; Fig. 5.9). Thus, low-ranking females tended to avoid feeding in high-quality but crowded patches (Nakagawa 1990). Similarly, on Koshima, high-ranking macaques dominated *Myrica rubra* fruits whose distribution is concentrated for longer periods of time, whereas such differences in food habits among different dominance ranks disappeared when macaques fed on an evenly distributed insect, *Geisha distinctissima* (Iwamoto 1987). At Takasakiyama, low-ranking macaques compensated for the lack of energy obtained from artificial foods (high-quality, patchy distribution) by feeding more frequently on natural foods (low-quality, sparse distribution) and by increasing the total number of food items (Soumah and Yokota 1991). Thus, the dominance relationship itself does not affect food preferences; instead, the characteristics of the food (abundance, distribution, and existence of other food items) cause dominance rank to come into play, often allowing high-ranking macaques to dominate preferred foods.

## 5.3 Ranging Behavior

Valuable places for primates, such as feeding sites, sleeping sites, water holes, and predator-free sites, are distributed heterogeneously and are limited in number (Wada and Tokida 1981; Cowlishaw 1997; Nakagawa 1999; Tsuji and Takatsuki 2004). Thus, similar to other species, groups of Japanese macaques establish their home range and daily travel distances within it to efficiently obtain food resources and to avoid predator or physical stresses such as strong wind and extremely high/low air temperatures. As a result, primates tend to use their home range unevenly. In addition, movements among several valuable locations determine daily travel distances. In this section, I review home range use, sleeping-site selection, and the daily travel distances of Japanese macaques, which comprise ranging behavior. I have not shown variations in interindividual ranging in this section because macaques move as members of their group and little variation occurs among individuals.

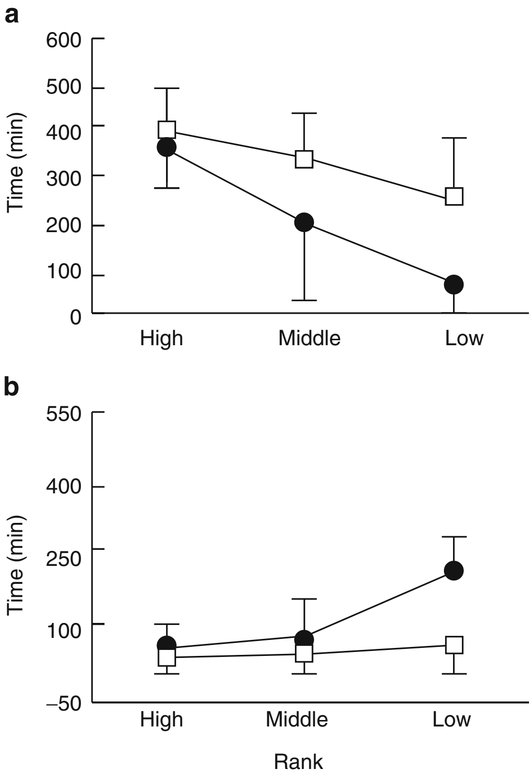

**Fig. 5.9** Effects of dominance rank (high, middle, low) and available patch size on foraging success on time allocation to feeding on *Zelkova* nuts (staple food in the autumn) (**a**) and *Carpinus* nuts (alternative food during the autumn) (**b**). *Open squares*, days when large patches of *Zelkova* nuts were available; *filled circles*, days when large patches of *Zelkova* nuts were not available. (From Saito 1996)

## 5.3.1 Regional Variation in Ranging Behavior

### 5.3.1.1 Home Range Use

Maruhashi et al. (1998) compared the home range use of Japanese macaques on Kinkazan with that of macaques living in the coastal forest of Yakushima and found that the Yakushima macaques intensively used a limited number of feeding sites. In fact, the macaques in the warm-temperate region spent half of their time and energy feeding only in 15–20% of their home range (Yakushima: Maruhashi 1986, Koshima: Iwamoto 1989), whereas macaques in the cool-temperate region used 22–30% of their home range in half of their time (Kinkazan: Tsuji and Takatsuki 2004). Food abundance was the main factor underlying this difference. The food density on Yakushima was estimated to be twice as high as that on Kinkazan; for example, the food tree density was 1,800 trees/ha on Yakushima and 90 trees/ha on Kinkazan (Maruhashi et al. 1998).

#### 5.3.1.2 Sleeping-Site Selection

Yoshihiro et al. (1979), Wada and Tokida (1981), and Wada et al. (2007) showed that the winter sleeping sites of the macaques in Shiga Heights were clustered around conifer trees such as the Japanese cedar (*Cryptomeria japonica*). In contrast, sleeping sites in the warm-temperate regions were located near the macaques' staple foods, and no effect of climate was detected (Takasakiyama: Itani and Tokuda 1954; Mt. Kawaradake: Ikeda et al. 1973; Minoo: Kanazawa and Yoshida 1982). Thus, both climate conditions and food environment determined sleeping-site selection in the cool-temperate zone, whereas only food environment determined the sleeping site in the warm-temperate zone.

#### 5.3.1.3 Daily Travel Distance

Table 5.1 shows the daily travel distances of the Japanese macaques (km/day). As a whole, the daily travel distances of the macaques inhabiting cool-temperate regions except in autumn were shorter than those of the macaques living in the warm-temperate regions. These differences were related to the food environment. In general, the food environment in the cool-temperate zones is poorer than that in the warm-temperate regions (see Sect. 5.3.1.1). The differences in travel distance indicate that the macaques in the cool-temperate regions use relatively low-cost/low-benefit tactics to obtain sparsely distributed food resources, whereas the macaques in the warm-temperate regions use relatively high-cost/high-benefit tactics to obtain densely distributed food resources.

Climate conditions can affect daily travel distances. In the cool-temperate region (Figs. 5.1 and 5.2) in winter, daily travel distances tend to be shorter in study sites with low temperatures and heavy snowfalls (Shimokita, Shiga Heights, Kamikochi) than in areas with relatively high temperatures and little snowfall (Kinkazan; Table 5.1). Snow prevents macaques from moving efficiently (Wada and Tokida 1981), and low temperatures increase the thermoregulatory cost (Hori et al. 1977). When traveling under these conditions, the macaques do not produce sufficient energy, and they must employ more low-cost/low-benefit tactics than the macaques living in areas with little snow (cf. Nakagawa 1989b).

### *5.3.2 Temporal Variation in Ranging Behavior*

#### 5.3.2.1 Seasonal Changes in Home Range Use

Many researchers have reported that the home range use of Japanese macaques changes seasonally both in the cool-temperate region (Shiga Heights: Wada and Ichiki 1980; Nikko: Koganezawa 1997; Kamikochi: Izumiyama 1999; Kinkazan: Tsuji and Takatsuki 2004) and in the warm-temperate region (Takasakiyama: Itani and Tokuda 1954; Mt. Kawaradake: Ikeda et al. 1973; Koshima: Iwamoto 1989;

**Table 5.1** Regional differences in daily travel distance (km/day)

| Habitat | Vegetation type | Group size | Snow depth (cm) | Season<br>Spring | <br>Summer | <br>Autumn | <br>Winter | Study year | Reference |
|---|---|---|---|---|---|---|---|---|---|
| Shimokita | D | 51–62 | 35 | 1.0 | – | – | 1.4 | 1981–1982 | Watanuki and Nakayama (1993) |
| Shimokita | D | 72–79 | 122 | 0.7 | – | – | 0.6 | 1983–1984 | Watanuki and Nakayama (1993) |
| Kinkazan | D | 32 | 0 | – | – | 1.9 | 1.1 | 1987–1988 | Nakagawa (1989b) |
| Shiga Heights | D | 24 | 165 | 0.7 | – | – | 0.6 | 1972 | Wada and Tokida (1981) |
| Shiga Heights | D | 41 | NA | 1.0 | 1.3 | 2.5 | 0.4 | 1974–1975 | Wada (1979) |
| Kamikochi | D | 68 | <200 | 1.8 | 2.2 | 2.5 | 0.7 | 1991–1997 | Izumiyama (1999) |
| Boso | D/E | 56 | – | – | 2.1 | 2.0 | 1.0 | 1970–1972 | Yotsumoto (1976) |
| Kawaradake | E | 99 | – | 1.2 | 2.1 | 1.2 | 1.4 | 1973 | Ikeda (1982) |
| Takasakiyama | E | 180 | – | 2.0 | – | 2.5 | 0.7 | 1950–1951 | Itani and Tokuda (1954) |
| Yakushima (coast) | E | 47 | – | – | 2.0 | 1.2 | – | 1976 | Maruhashi (1981) |
| Mean (SD) | | | | **1.2** (0.5) | **2.0** (0.4) | **2.0** (0.6) | **0.9** (0.4) | | |
| Mean (SD) for deciduous forest | | | | **1.0** (0.5) | **1.9** (0.5) | **2.2** (0.3) | **0.8** (0.3) | | |
| Mean (SD) for evergreen forest | | | | **1.6** (0.5) | **2.0** (0.1) | **1.6** (0.8) | **1.1** (0.5) | | |

Spring, March–May; summer, June–August; autumn, September–November; winter, December–FebruaryD, deciduous forest; E, evergreen forest

Fukaya et al. 2002; Go, 2010). Similar to other nonhuman primate species (e.g., Barton et al. 1992 for savanna baboons *Papio ursinus*; Nakagawa 1999 for patas monkeys *Erythrocebus patas* and savanna monkeys *Cercopithecus aethiops*), the seasonal changes in home range use are driven primarily by the food environment.

In general, range shifts are correlated with dietary changes (Hemingway and Bynum 2005). At Kinkazan, for example, the home range location and its use were affected by the distribution of staple foods in a given season (Tsuji and Takatsuki 2004; Fig. 5.10). In addition, Fukaya et al. (2002) and Go (2010) found that the distribution of not just one single food item, but that of several food items, affected the seasonal home range use by macaques on Koshima.

The home range of Japanese macaques in the cool-temperate zone changes not only horizontally but also vertically. At Mt. Yarigatake, for example, macaques move from approximately 1,300 m a.s.l. in the winter to approximately 3,000 m a.s.l. in the summer (Izumiyama 2002) (for photograph, see Fig. 3.9). Similar vertical movements have also been reported at Nikko (Koganezawa 1997) and Shiga Heights (Wada and Ichiki 1980) and have been attributed to altitudinal differences in food availability or snowfall or both.

Predation affects the ranging behavior of some primate species (Cowlishaw 1997); however, Japanese macaques currently have virtually no predators (Oi 2002 but see Iida 1999), and thus this effect is negligible.

#### 5.3.2.2 Yearly Changes in Home Range Use

On Kinkazan, Tsuji and Takatsuki (2009) observed yearly variation in the location and use of the macaque home range (Fig. 5.11) caused primarily by yearly variation in nut-fruiting (see Fig. 5.7). In contrast, the winter home ranges of macaques at Mt. Yarigatake were stable from year to year (Izumiyama 2002). The large amount of snowfall at Mt. Yarigatake may mask the effect of yearly changes in the food environment.

Several other factors affect yearly changes in macaque ranging. The first is habitat deterioration caused by the macaques themselves: Japanese macaques in Shimokita shifted their home range from old sites where the productivity of *Morus bombycis* buds was low to new sites where many *Morus* trees grew (Watanuki et al. 1994). Similarly, at Shiga Heights, macaques shifted their home range because of the death of their staple food trees (Wada 1983). The second factor is human activity: at Nikko, provisioning by tourists altered the location and use of the macaque home range (Koganezawa and Imaki 1999), leading to a rather unfortunate consequence: in years of heavy snowfall, this macaque population suffered mass mortality as a result of malnutrition (the numbers of tourists decrease during winters with heavy snow). At Shimokita, on the other hand, the spraying of weed killer caused a habitat disturbance, which, in turn, shifted the home range of macaques (Izawa 1971). A third factor is the effect of other groups. At Mt. Hakusan, the home ranges of many groups living along the gorge changed yearly, likely a consequence of the existence of adjacent groups (Takizawa 2002).

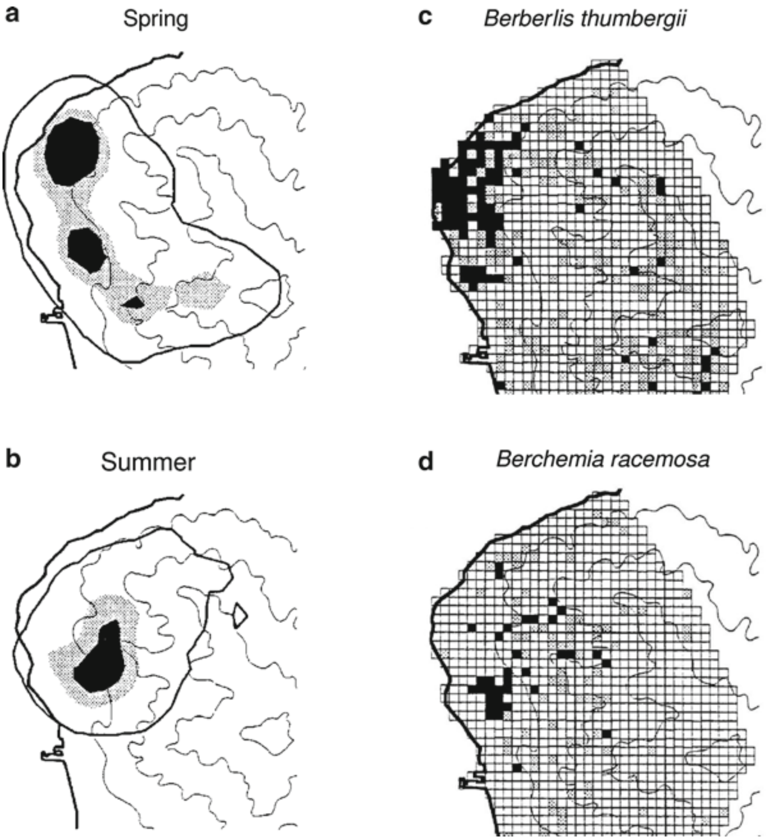

**Fig. 5.10** Home ranges (*solid lines*, fixed kernel methods, 95%) and core areas (fixed kernel methods: *dotted squares*, 50%; *shadowed squares*, 25%) of group A at Kinkazan in spring (**a**) and summer (**b**) and distributions of the staple food (*dotted squares*, high coverage; *shadowed squares*, low coverage): *Berberis thunbergii* (leaves and flowers) is a staple food in the spring (**c**), and *Berchemia racemosa* (fruits) is a staple food in the summer (**d**). The quadrat size is 50 × 50 m; contours indicate 100 m interval or every 100 m (From Tsuji and Takatsuki 2004)

#### 5.3.2.3 Seasonal Changes in Sleeping-Site Selection

In Shiga Heights, the winter sleeping sites were located in concentrated depressions on slopes (distribution in a limited band 300 m from the valley) among clusters of conifer trees (Yoshihiro et al. 1979; Wada and Tokida 1981). These sites protect the macaques from severe climate conditions such as snowfall and low temperatures, and their sleeping sites change in the spring. In contrast, sleeping sites in the warm-temperate regions were located near staple foods and did not change with the season (Takasakiyama: Itani and Tokuda 1954; Kawaradake: Ikeda et al. 1973; Minoo: Kanazawa and Yoshida 1982).

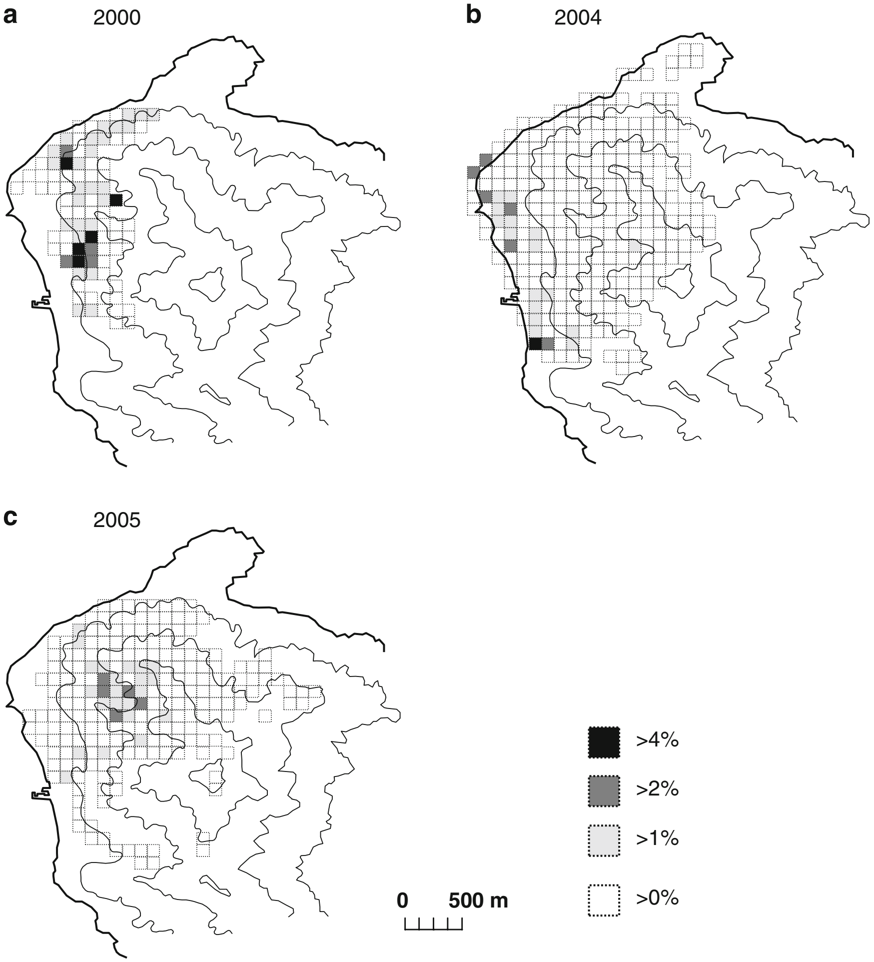

**Fig. 5.11** Autumn home range use of group A on Kinkazan in 2000 (**a**), 2004 (**b**), and 2005 (**c**). The intensity of use is expressed as the relative frequency (%). Contours indicate 100 m interval or every 100 m. The quadrat size was 100 × 100 m. (From Tsuji and Takatsuki 2009)

### 5.3.2.4 Seasonal Changes in Daily Travel Distance

The daily travel distances of Japanese macaques (m/day) show clear seasonal changes: as a whole, the distances are longest in summer and autumn, followed by spring, and shortest in winter (Table 5.1). Furthermore, the distances in the cool-temperate zone are longest in autumn, summer in second, spring in third, and shortest in winter, whereas the distances in the warm-temperate zone are longest in summer, followed by autumn and spring, and shortest in winter. Climate conditions also affect the daily travel distance. Temperature, wind strength, and snow depth have been reported to decrease the daily travel distance in Kamikochi, Shimokita, and Shiga Heights, respectively (Wada and Tokida 1981; Watanuki and Nakayama 1993; Izumiyama 1999).

Seasonal changes in the macaque daily travel distance, therefore, can be attributed to seasonal changes in feeding tactics: macaques use high-cost/high-benefit tactics in summer (warm-temperate zone) and autumn (cool-temperate zone) when many fruits are available and climate conditions are moderate, whereas in winter when few food resources are available and external factors are severe, they use low-cost/low-benefit tactics. However, relationships between the food environment and the moving distances are complicated, and no study about this topic has been conducted.

#### 5.3.2.5 Yearly Changes in Daily Travel Distance

In addition to seasonal changes, daily travel distance is influenced by year-to-year changes in climate conditions and human impact. For example, the daily travel distance in winter at Shimokita was longer in 1981–1982 (1.4 km) when little snow fell (35 cm) than in 1983–1984 (0.6 km) when the snow depth was unusually great (122 cm) (Watanuki and Nakayama 1993; see Table 5.1).

## 5.4 Activity Budgets

Japanese macaques are diurnal, and they repeat the activities of moving, feeding, and sometimes resting throughout daylight hours (Yotsumoto 1976; Maruhashi 1981; Iwamoto 1982). Foods vary in their physical characteristics, nutritional content, and spatial distribution, and, consequently, the cost of foraging, in terms of searching and handling, and the nutritional benefits obtained, differ among food items. This variation is likely to affect the amount of time allocated to each activity, that is, the activity budget, to balance the costs and benefits of foraging for different food items (Agetsuma 1995a).

### *5.4.1 Regional Variation in Activity Budgets*

Agetsuma and Nakagawa (1998) compared the activity budgets of Japanese macaques on Kinkazan with those of macaques living in the coastal forest of Yakushima and found that the time spent feeding on Kinkazan was 1.7 times greater than on Yakushima because of higher demand of energy for thermoregulation and lower intake rate of energy from foods. These findings suggest that the percentage of feeding time is higher in the cool-temperate zone than in the warm-temperate zone (Table 5.2). The percentage of feeding time did not exceed 75% in either region (Table 5.2), and this value may represent the threshold for

**Table 5.2** Seasonal changes in feeding time percentage in different habitats

| Habitat | Vegetation type | Season Spring | Summer | Autumn | Winter | Study year | Reference |
|---|---|---|---|---|---|---|---|
| Shimokita | D | 36.5 | – | – | 36.5 | 1984 | Watanuki and Nakayama (1993) |
| Kinkazan | D | – | – | 34.4 | 56.0 | 1984–1985 | Nakagawa (1989a) |
| Kinkazan | D | – | – | 54.4 | – | 1985 | Nakagawa (1989a) |
| Kinkazan | D | – | – | 73.0 | 70.0 | 1987–1988 | Nakagawa (1989b) |
| Kinkazan | D | 54.6 | 43.4 | – | – | 1991–1992 | Nakagawa (1994) |
| Shiga Heights | D | 37.3 | 24.8 | – | 40.2 | 1962–1963 | Suzuki (1965) |
| Shiga Heights | D | 34.7 | – | – | 24.3 | 1972 | Wada and Tokida (1981) |
| Boso | D/E | – | – | 26.0 | 28.9 | 1970–1972 | Yotsumoto (1976) |
| Takasakiyama | E | – | 26.6 | – | 41.7 | 1987–1988 | Soumah and Yokota (1991) |
| Takasakiyama | E | 37.4 | – | – | 24.6 | 1985–1986 | Yokota (1989) |
| Koshima | E | 49.5 | – | 45.6 | 44.4 | 1977–1978 | Iwamoto (1982) |
| Koshima | E | – | 39.3 | 39.2 | 37.1 | 1984 | Iwamoto (1992) |
| Yakushima (coast) | E | 30.8 | 19.9 | – | 47.3 | 1990–1991 | Agetsuma (1995b) |
| Yakushima (coast) | E | 38.1 | – | 24.8 | 28.2 | 1991–1992 | Agetsuma (1995b) |
| Yakushima (coast) | E | – | – | 45.7 | 54.0 | 1994–1995 | Domingo-Roura and Yamagiwa (1999) |
| Yakushima (coast) | E | 29.9 | 22.4 | 27.3 | 30.5 | 1997–1998 | Hanya (2003) |
| Yakushima (coniferous forest) | E | 45.8 | 32.7 | 39.5 | 41.6 | 2000–2001 | Hanya (2004b) |
| Mean (SD) | | **39.5** (8.0) | **29.9** (8.9) | **41.0** (14.8) | **40.3** (12.8) | | |
| Mean (SD) for deciduous forest | | **40.8** (9.3) | **34.1** (13.2) | **53.9** (19.3) | **45.4** (17.8) | | |
| Mean (SD) for evergreen forest | | **38.6** (7.9) | **28.2** (7.9) | **37.0** (9.0) | **38.8** (9.6) | | |

Spring, March–May; summer, June–August; autumn, September–November; winter, December–FebruaryD, deciduous forest; E, evergreen forest feeding time because macaques must allocate time to other activities such as moving and resting.

In addition, Agetsuma and Nakagawa (1998) found that the social grooming time was 1.9 times greater on Yakushima than on Kinkazan. Differences in grooming time may affect the social bonding of group members (Nakagawa 1998). Between-group competition is severe on Yakushima (Saito et al. 1998), and the longer grooming times may have contributed to the promotion of coalition among adult females, which favors between-group competition

## *5.4.2 Temporal Variation in Activity Budgets*

### 5.4.2.1 Seasonal Changes in Activity Budgets

Table 5.2 shows seasonal changes in the time spent feeding. The percentage of time spent feeding was generally shorter in spring and summer compared to autumn and winter, although large variation was observed among the study sites (Table 5.2). Seasonal changes in macaque foraging tactics may underlie the seasonal changes in feeding time. Agetsuma (1995b) and Agetsuma and Nakagawa (1998) conducted detailed analyses of the relationship between feeding time for each food category and total feeding time (as benefit) or moving time (as cost of foraging) of the macaques on Kinkazan and in the coastal forest of Yakushima. They found that the macaques in both habitats increased their moving time and decreased their feeding time when relatively high-quality food items such as fruits and insects (high-cost/high-benefit tactics) were available, whereas they decreased moving time and increased total feeding time when only relatively low-quality food items such as mature leaves, buds, and bark (low-cost/low-benefit tactics) were available. Considering the seasonal change in food habits (Fig. 5.4; see also Sect. 5.2.2.1), the macaques on Yakushima and Kinkazan were more likely to use high-cost/high-benefit tactics in the autumn, when high-quality food items such as fruit were available, and low-cost/low-benefit tactics in the winter, when they ate low-quality food items. Furthermore, Hanya (2004b) found that the macaques decreased the percentage of feeding time when the feeding rate (represented by the number of ingested food items per unit time) and abundance of staple foods increased.

Several studies have evaluated the effect of climate conditions (air temperature and snowfall) on the activity of the macaques. In response to decrease in air temperature, macaques in the coastal forest of Yakushima increased their feeding time and decreased moving time (Agetsuma 1995b). Similarly, in Shimokita, macaques increased their resting time and decreased their moving time in the winter (Watanuki and Nakayama 1993). In Shimokita, snowfall affected macaque activity levels such that they decreased the time spent moving after heavy snowfall (Watanuki and Nakayama 1993). Hanya (2004b) found that macaques in the coniferous forest of Yakushima decreased both feeding and moving when the temperature was low. The temperature is lower in the coniferous forest than in the coastal forest of the island,

and this factor likely forced the macaques to decrease feeding time to maintain their body temperature (Hanya 2004b). These results suggest that the effect of the thermoregulatory/moving cost of the activity of feeding is at least as great as that of food-related factors per se.

To determine if there are rules for time allocation for each behavioral category in each month, Agetsuma and Nakagawa (1998) suggested synthetic relationships among day length, feeding, moving, resting, and social grooming of the macaques on Kinkazan and in the coastal forest of Yakushima. They suggested the following formulas:

$$\text{Kinkazan: REST} = 0.85\text{DAY} - 0.77\,(\text{FEED} + \text{MOVE}) - 1.49,$$
$$\text{Yakushima (coastal forest): REST} = 0.71\text{DAY} - 0.41(\text{FEED} + \text{MOVE}) - 0.32$$

where REST, FEED, and MOVE are the time spent resting, feeding, and moving (h), respectively, and DAY is day length (h). The results suggest that resting time can be converted into additional feeding time whenever required. These formulas imply that for the macaques on Kinkazan (and perhaps in all cool-temperate regions) it is difficult to secure enough time to rest compared to the macaques in the coastal forest of Yakushima (and perhaps in all warm-temperate regions), suggesting that life in the cool-temperate region is more severe.

#### 5.4.2.2 Yearly Changes in Activity Budgets

In tropical regions, several studies have reported that yearly environmental changes affect activity budgets (Whitten 1983 for savanna monkeys; Alberts et al. 2005 for savanna baboons, *Papio anubis*), indicating that the time devoted to social activity changed yearly. For Japanese macaques, systematic studies of yearly changes in activity budgets are limited, and only qualitative data have been collected. For example, on Kinkazan and in the coastal forest of Yakushima, the percentage of time spent feeding in the autumn and winter changed yearly (see Table 5.2), which may be attributed to yearly changes in nut-fruiting (see Fig. 5.7) and consequent yearly differences in the cost of searching for nuts. In Shimokita, on the other hand, the percentage of time spent moving on the ground increased during years of little snow (Watanuki and Nakayama 1993).

### *5.4.3 Interindividual Variation in Activity Budgets*

#### 5.4.3.1 Effects of Age and Sex

On Yakushima and Kinkazan, the time spent feeding did not differ among age classes (Hashimoto 1991; Agetsuma 2001; Hanya 2003). In contrast, in Shimokita, juvenile macaques increased their feeding times when eating dormant buds and bark, whereas adult females did not (Nakayama et al. 1999). In this case, the adults may have been minimizing their energy cost. As for sexual differences, the percentage of time spent feeding by adult males in the autumn was shorter than that of adult females in Shimokita. Similarly, on Koshima, the feeding time of males was shorter than that of females (Iwamoto 1987). In the coastal forest of Yakushima, the resting time of males was longer than that of females, whereas the grooming time of males was shorter (Agetsuma 2001). These differences may potentially reflect a male mating tactic to minimize time spent feeding (Iwamoto 1987). On the other hand, female sexual proceptivity affected their activity budgets. In the coastal forest of Yakushima, periovulatory females who copulated with multiple males decreased feeding time to half that spent on anestrous days. However, when they copulated only with high-ranking males, no difference in feeding time was observed (Matsubara and Sprague 2004).

### 5.4.3.2 Effects of Dominance Rank

Among the male macaques on Koshima, the feeding time of high-ranking males was shorter than that of low-ranking males because the former fed more frequently on high-quality artificial foods, such as wheat (Iwamoto 1987). Similarly, the feeding time of a highest ranking male was shorter than that of subordinate males in the coastal forest in Yakushima (Matsubara 2003). In contrast, feeding times did not differ among females, except when they were eating *M. rubra* fruits, whose distribution was clumped (Iwamoto 1987): in this case, high-ranking females harvested this food item for a longer period of time than did low-ranking females. Thus, the effects of the female dominance rank on feeding times were visible only when food monopolization by high-ranking animals was possible. Soumah and Yokota (1991) noted that low-ranking females compensated for this disadvantage by (1) lengthening their feeding time, (2) increasing the number of food items they ingested, and (3) increasing their feeding rate. Such efforts by low-ranking females may reduce the time spent on other activities, consequently leading to deficiencies in reproductive activity. However, no studies demonstrating these deleterious reproductive effects were conducted.

## 5.5 Future Challenges

In this chapter, I introduced both regional and temporal variation in the feeding ecology of Japanese macaques. The advance of ancestral Japanese macaques to the Japanese archipelago appears to have been enhanced by certain morphological, physiological, and behavioral traits. Among these, regional and temporal variation in the feeding ecology of Japanese macaques can be considered behavioral traits aimed at adapting to both regular (seasonal) and irregular (yearly) environmental fluctuations.

I have also shown interindividual variations in macaque feeding ecology in this chapter. Japanese macaques, especially females, live as members of their group.

Being a member of a group is advantageous for obtaining food resources and avoiding severe aggression from conspecifics (Wrangham 1980). However, in this arrangement, every individual is bound in a complex interindividual relationship. Thus, the ability of individuals to flexibly adjust their behavioral patterns according to their social status is an important trait for living in the temperate region. Dominance rank differed from other social factors (age and sex) in the indirect nature of its effect, which varied based on food characteristics (Saito 1996). Rank-related feeding success is likely to ultimately affect macaque population parameters, but relevant studies are quite limited (Tsuji 2007).

In conclusion, two pending challenges to the study of the feeding ecology of Japanese macaques should be highlighted. First, quantitative data concerning food environment and climate conditions are quite lacking. As noted earlier, we now understand that yearly changes in the food environment (Komiyama et al. 1991; Noma 1996; Suzuki et al. 2005) and in climate conditions affect food habits (Watanuki and Nakayama 1993; Tsuji et al. 2006; see Sect. 5.2.2), ranging (Hill and Agetsuma 1995; Tsuji and Takatsuki 2004, see Sect. 5.3.2), and activity budgets (Watanuki and Nakayama 1993; Hill and Agetsuma 1995, see Sect. 5.4.2) of Japanese macaques. Unfortunately, these data have been collected quantitatively at only a few study sites. To generalize the adaptive meaning of the observed feeding ecology to regional and temporal changes, it is essential to conduct systematic, long-term studies at other sites that combine detailed observations of the macaques and monitoring of temporal fluctuations in their environment.

Another challenge is to extend regional comparisons of Japanese macaque feeding ecology. Several comparative studies of the feeding ecology of Japanese macaques have been conducted (Suzuki 1965; Uehara 1975; Nakagawa et al. 1996; Agetsuma and Nakagawa 1998; Maruhashi et al. 1998), and the relationships between food environment–climate conditions and feeding ecology of the macaques have been evaluated. However, no studies have addressed the effect of snowfall, yearly change in food environment, and interindividual variations on feeding ecology. Furthermore, no studies have been conducted to investigate the factors affecting food habits at the individual study sites. As noted earlier in this chapter, the vegetation and climate conditions (see Fig. 5.1) in Japan are quite diverse, thus facilitating the detection of the effects of food environment and climate conditions on the feeding ecology of macaques. With the long-term data accumulated for various sites, researchers can certainly form an interesting and relevant theory that is generally applicable not only to other primate species but also to group-living animals inhabiting temperate regions.

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# Chapter 6: Seed Dispersal by Japanese Macaques

**Tatsuya Otani**

## 6.1 Introduction

Seed dispersal is a crucial process in recruitment of plant populations, as well as for pollen dispersal. The location of dispersed seeds affects the survival of seedlings and the spatial distribution pattern of plants. Plants employ various strategies for effective seed dispersal, and diaspores have unique structures that utilize biotic and/or abiotic factors such as fleshy arils for endozoochory, thorny hooks for epizoochory, and membrane wings for anemochory. Most studies on seed dispersal by mammals have concerned endozoochory, that is, when an animal eats the edible fleshy parts surrounding seeds and then disseminates intact seeds by defecating or spitting out the seeds, although a few studies have examined epizoochory (e.g., Mouissie et al. 2005). The viability or survival rate of seeds can be altered at each step of seed dispersal and recruitment process, starting from fruit foraging by animals, followed by seed passage through digestive tracts, seed deposition on the forest floor, germination, and finally seedling establishment (Schupp 1993). Numerous studies have reported that diverse primate species act as effective endozoochorous seed dispersers for tree species in tropical and subtropical forests (Balcomb and Chapman 2003; Russo et al. 2006). We have only one indigenous primate species, *Macaca fuscata*, in Japan, and previous studies have suggested that Japanese macaques are also effective agents of seed dispersal for tree species that compose the cool- and warm-temperate forests in Japan. In this chapter, I present findings from previous studies on seed dispersal by Japanese macaques.

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## 6.2 Fleshy-Fruited Species in Southern and Northern Japan

Species compositions of forest trees are widely different at the southern and northern ends of the Japanese macaques range in Japan. At the southern end, warm-temperate evergreen broad-leaved forests dominated by species of Lauraceae, Myrsinaceae, Moraceae, and Fagaceae cover the lowlands of Yakushima Island (Miyawaki 1980). At the other end, cool-temperate deciduous broad-leaved forests dominated by species of Fagaceae, Aceraceae, Betulaceae, and Pinaceae are found widely in the snowy region of northern Honshu Island (Miyawaki 1987). Soft and juicy parts of fruits, formed from various tissues such as aril, mesocarp, endocarp, and sepal, are considered as adaptations for endozoochory (Willson et al. 1989). The percentage of fleshy-fruited tree species of the total tree species found in a forest stand decreases with increase in latitude (Willson et al. 1989; Herrera 2002). In Japan, the percentage of fleshy-fruited woody species in evergreen broad-leaved forests in southern areas (mean, 71%) is higher than that in deciduous broad-leaved forests in northern areas (mean, 50%), and deciduous arbor species comprise a significantly lower number of fleshy-fruited species (37%) than other life forms such as evergreen arbors, evergreen and deciduous shrubs, and vines (53–68%; Otani 2005). These facts imply that animal seed dispersers can contribute to the recruitment process of more tree species in the southern part of Japan than in the northern part, and the potential importance of animal seed dispersers for fleshy-fruited plants in forests is greater in evergreen forests than in deciduous forests.

## 6.3 Plant Species Dispersed by Japanese Macaque Feces

Fecal analysis is a simple and reliable method for determining the type and frequency of seeds dispersed by animals. Tables 6.1 and 6.2 show the frequency of occurrence and number of seeds extracted from Japanese macaque feces collected at the western lowland of Yakushima Island and the northern part of Honshu Island, respectively. From the western lowland of Yakushima (30°20′N, 130°30′E), which is covered by primary and secondary broad-leaved evergreen forests, 34 species in 19 families including 31 fleshy-fruited species were reported to be dispersed by feces, and a fecal sample contained seeds of 2.8 ± 1.4 species on average (Table 6.1). Several hundred seeds were found in a fecal sample for the top four species: *Ficus superba* var. *japonica*, *Ficus thunbergii*, *Eurya emarginata*, and *Eurya japonica*. Hanya et al. (2003) also reported other seed species found in macaque feces in the lowland of Yakushima, such as *Ficus pumila*, *Euscaphis japonica*, and *Distylium racemosum*. At the two sites in the northern part of the Honshu Island, Kashima (37°42′N, 140°50′E) and Shimokita Peninsula (41°09′N, 140°47′E), seeds of 21 species in 16 families were extracted from fecal samples (Table 6.2). The number of seed species in a fecal sample averaged 2.4 ± 1.5 in Kashima and 1.9 ± 0.8 in Shimokita. Mean numbers of seeds per fecal sample exceeded 900 for tiny-seeded

**Table 6.1** Frequency of occurrence and number of seeds in Japanese macaques' feces collected at the western coastal area of Yakushima Island

| Species | Family | Life form | Frequency of occurrence | Number of seeds per feces (±SD) |
|---|---|---|---|---|
| *Ficus superba* var. *japonica* | Moraceae | Tree | 0.52 | 456 ± 617 |
| *Ficus thunbergii* | Moraceae | Vine | 0.47 | 323 ± 374 |
| *Eurya emarginata* | Theaceae | Shrub | 0.32 | 277 ± 286 |
| *Eurya japonica* | Theaceae | Shrub | 0.26 | 284 ± 370 |
| *Actinidia rufa* | Actinidiaceae | Vine | 0.23 | 60 ± 69 |
| *Ficus erecta* | Moraceae | Shrub | 0.20 | 58 ± 76 |
| *Psychotria serpens* | Rubiaceae | Vine | 0.17 | 29 ± 32 |
| *Cleyera japonica* | Theaceae | Shrub | 0.11 | 51 ± 77 |
| *Elaeocarpus japonicus* | Elaeaocarpaceae | Tree | 0.05 | 8 ± 7 |
| *Vaccinium bracteatum* | Ericaceae | Shrub | 0.04 | 18 ± 13 |
| *Ficus nipponica* | Moraceae | Vine | 0.03 | 82 ± 43 |
| *Morinda umbellata* | Rubiaceae | Vine | 0.03 | 10 ± 10 |
| *Actinodaphne longifolia* | Lauraceae | Tree | 0.03 | 2 ± 1 |
| *Schefflera octophylla* | Araliaceae | Tree | 0.02 | 12 ± 1 |
| *Ampelopsis brevipedunculata* | Vitaceae | Vine | 0.02 | 11 ± 6 |
| *Vitis flexuosa* | Vitaceae | Vine | 0.02 | 7 ± 7 |
| *Callicarpa japonica* | Verbenaceae | Shrub | 0.02 | 2 ± 0 |
| *Ternstroemia gymnanthera* | Theaceae | Tree | 0.02 | 71 ± 70 |
| *Rubus grayanus* | Rosaceae | Shrub | 0.02 | 21 ± 12 |
| *Parthenocissus tricuspidata* | Vitaceae | Vine | 0.02 | 16 ± 10 |
| *Myrica rubra* | Myricaceae | Tree | 0.02 | 16 ± 11 |
| *Myrsine seguinii* | Myrsinaceae | Shrub | 0.02 | 11 ± 2 |
| *Ardisia sieboldii* | Myrsinaceae | Tree | 0.02 | 9 ± 8 |
| *Pittosporum tobira* | Pittosporaceae | Shrub | 0.02 | 3 ± 3 |
| *Psychotria rubra* | Rubiaceae | Shrub | 0.02 | 2 |
| *Diospyros morrisiana* | Ebenaceae | Tree | 0.02 | 1 |
| *Mallotus japonicus*[a] | Euphorbiaceae | Tree | <0.01 | 188 |
| *Picrasma quassioides*[a] | Simaroubaceae | Tree | <0.01 | 23 |
| *Dendropanax trifidus* | Araliaceae | Tree | <0.01 | 17 |
| *Symplocos lucida* | Symplocaceae | Tree | <0.01 | 11 |
| *Cinnamomum camphora* | Lauraceae | Tree | <0.01 | 4 |
| *Citrus* sp. | Rutaceae | Shrub | <0.01 | 2 |
| *Vitis ficifolia* var. *lobata* | Vitaceae | Vine | <0.01 | 1 |
| Unknown | | | <0.01 | 2 |

Species are arranged in decreasing order by frequency of occurrence. Number of seeds per feces was calculated on the basis of the mean fresh weight of a feces (15.3 gfw). Frequency of occurrence, proportion of number of feces including seeds to the total number of feces collected ($n = 132$)

[a] Not fleshy fruits

*Source:* Modified from Otani (2005)

**Table 6.2** Frequency of occurrence and number of seeds in Japanese macaques' feces collected at two sites (Kashima and Shimokita) in northern Japan

| Species | Family | Life form | Frequency of occurrence | Number of seeds per feces (±SD) | |
|---|---|---|---|---|---|
| | | | | Kashima | Shimokita |
| *Actinidia arguta* | Actinidiaceae | Vine | 0.55 | 156 ± 215 | 905 ± 1,029 |
| *Actinidia polygama* | Actinidiaceae | Vine | 0.28 | 992 ± 764 | 1,408 ± 1,299 |
| *Vitis coignetiae* | Vitaceae | Vine | 0.19 | 27 ± 25 | 20 ± 32 |
| *Akebia trifoliata* | Lardizabalaceae | Vine | 0.16 | 98 ± 71 | 2 |
| *Rubus phoenicolasius* | Rosaceae | Shrub | 0.14 | 2,522 ± 1,787 | 299 ± 328 |
| *Berchemia racemosa* | Rhamnaceae | Vine | 0.09 | 4 ± 3 | 108 ± 88 |
| *Schisandra repanda* | Schisandraceae | Vine | 0.09 | 3 ± 3 | 4 ± 2 |
| *Calliearpa japonica* | Verbenaceae | Shrub | 0.08 | 30 ± 31 | 29 ± 19 |
| *Broussonetia kazinoki* | Moraceae | Shrub | 0.07 | 142 ± 114 | – |
| *Morus australis* | Moraceae | Shrub | 0.05 | 39 ± 29 | – |
| *Rubus palmatus* var. *coptophyllus* | Rosaceae | Shrub | 0.05 | 470 ± 196 | – |
| *Polygonum filiforme*[a] | Polygonaceae | Herb | 0.03 | 9 ± 3 | 366 ± 298 |
| *Stachyurus praecox* | Stachyuraceae | Shrub | 0.03 | 8 ± 9 | – |
| *Acanthopanax sciadophylloides* | Araliaceae | Tree | 0.03 | 85 ± 49 | – |
| *Cornus kousa* | Cornaceae | Tree | 0.02 | – | 11 ± 9 |
| *Oryza sativa*[a] | Gramineae | Herb | 0.01 | 1 ± 1 | – |
| *Ilex macropoda* | Aquifoliaceae | Tree | <0.01 | 174[b] | – |
| *Viburnum dilatatum* | Caprifoliaceae | Shrub | <0.01 | – | 3 |
| *Cornus brachypoda* | Cornaceae | Shrub | <0.01 | 1 | – |
| *Celastrus orbiculatus* | Celastraceae | Vine | <0.01 | – | 2 |
| *Prunus* sp. | Rosaceae | Tree | <0.01 | 1 | – |

Species are arranged in decreasing order by frequency of occurrence. Number of seeds per feces was calculated on the basis of mean volume of feces (13.9 ml)

Frequency of occurrence, proportion of number of feces including seeds to the total number of feces collected ($n = 182$)

[a] Not fleshy fruits

[b] Showing total number of seeds in a feces, because of the lack of data on feces volume

*Source:* After Otani (2003)

species of *Actinidia* and *Rubus* (1–2 mm in diameter). As for the life form of dispersed species, vines and shrubs dominate the species lists of Tables 6.1 and 6.2, with fewer tree species reported in Table 6.2 (4 species) than in Table 6.1 (13 species). The macaques in the northern Japanese sites used more disturbed and unforested lands than in Yakushima, because both the sites in northern Japan are covered by a mosaic of farmland, logged areas, conifer plantations, and secondary forests dominated by *Quercus serrata*, *Pinus densiflora*, and *Abies firma* in Kashima, and *Fagas crenata*, *Quercus crispula*, and *Thujopsis dolabrata* var. *hondai* in Shimokita; this might be one reason why so few species of trees are served by the macaques as endozoochorous seed dispersers.

Tsuji et al. (in preparation) found that seeds of at least 36 species in 22 families, including 20 fleshy-fruited species, were dispersed by macaque feces in Kinkazan Island, located off the Pacific shore of northern Japan. The forest in this island was relatively less disturbed by human activities. The top 5 major species in frequency of occurrence were *Viburnum dilatum*, *Rosa multiflora*, *Berchemia racemosa*, *Swida macrophylla*, and *Carpinus* sp., and the plant species list included 11 tree species, followed by six shrub and five vine species. These findings suggest that the macaques can act as seed dispersers for arbor species in undisturbed forests of northern Japan as for many species in the lowland of Yakushima.

## 6.4 Two Modes of Seed Dispersal

In addition to seed dispersal by their feces, Japanese macaques can disseminate seeds of fleshy fruits by spitting them out. They can store fruits in cheek pouches and then spit seeds out while moving or resting at remote sites away from foraged trees (Fig. 6.1). Yumoto et al. (1998) listed 19 species in 12 families, including three species of acorn, the seeds of which were dispersed by Yakushima macaques via cheek pouch. Except for the acorn species, all other species had relatively large-sized seeds ranging from 2.7 to 9.9 mm in diameter. Yumoto et al. (1998) reported that seeds of these fleshy-fruited species were also found in macaque feces but that larger-seeded species were less likely than smaller-seeded species to be found in feces. Although there is no report of seed spitting behavior in the northern areas, Tsuji et al. (in preparation) found relatively large fleshy-fruited seeds such as *Schisandra nigra*, *Cornus kousa*, *Diospyros lotus*, and *Prunus* sp. in fecal samples from Kinkazan. The seed size of these species (4.4–7.8 mm) is comparable to that of species dispersed via cheek pouch in Yakushima Island; therefore, these seeds may also be dispersed by spitting behavior of the macaques in northern Japan.

Seed handling of fleshy-fruited species by Yakushima macaques was classified into three groups, namely, swallowing, crunching, and spitting, and the morphological characteristics of the fleshy fruits were one of the determinants for the seed-handling techniques (Otani and Shibata 2000). Figure 6.2 shows the result of linear discriminant analysis for the relationship between the morphological characteristics of fruit and the seed-handling techniques of Yakushima macaques. It can be seen

**Fig. 6.1** A young Yakushima macaques, *Macaca fuscata yakui*, with enlarged cheek pouch storing fruits. This behavior leads to seed dispersal by spitting out

that the swallowing and spitting groups are reflected in linear discriminant function 1 (LDF 1), which correlates positively with seed size, and crunching and other groups, that is, seed predation and seed dispersal, are reflected in LDF 2, which correlates positively with fruit size and flesh volume relative to total fruit volume. For example, *Vaccinium bracteatum* produces flesh-rich fruit with tiny seeds that are swallowed and then dispersed by feces. Other factors, such as seed hardness and plant secondary metabolites in seeds, also influence the foraging behavior and the seed-handling techniques of primates (Kinzey and Norconk 1993). Further research is required to fully understand the relationship between the characteristics of fleshy fruits and the seed-handling techniques of Yakushima macaques.

## 6.5 Seed Destruction by Japanese Macaques

Seeds of fleshy fruits must be ingested and defecated intact by the macaques for successful seed dispersal. However, seeds of flesh-poor fruits (e.g., *Rhaphiolepis indica* var. *umbellata*; Fig. 6.2) can also be targets of foraging. Cracked and fragmented seeds of *Akebia trifoliata*, *B. racemosa*, and *Prunus* sp. were found in the feces of macaques from northern Japan along with intact seeds (Otani 2003). Thus, Japanese macaques act as seed predators as well as endozoochorous seed dispersers. It is difficult to assess the effect of fruit foraging and seed passage through digestive tracts on survival proportion of ingested seeds under field conditions. A fruit-feeding experiment was conducted with four captive Japanese macaques that were given known number of *E. emarginata* fruits, which is typically a endozoochorous fruit, to estimate the accurate proportion of seeds defecated

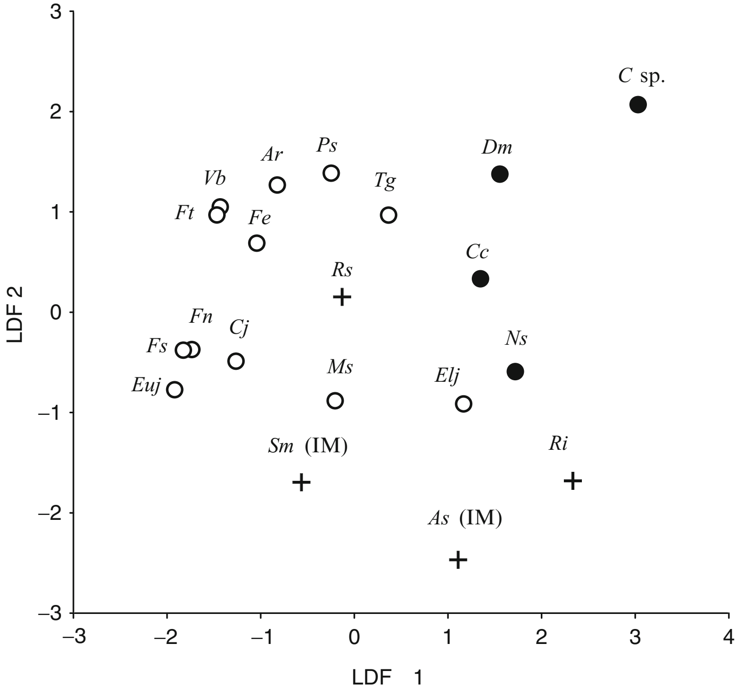

**Fig. 6.2** The results of linear discriminant analysis for the relationships between the characteristics of fleshy fruits and the seed-handling techniques of Yakushima macaques. The seed-handling techniques were classified into three categories: swallowing (*open circle*), crunching (*cross*), and spitting (*solid circle*). The abbreviated names of analyzed species are as follows: *Ft*, *Ficus thunbergii*; *Fs*, *Ficus superba* var. *japonica*; *Fn*, *Ficus nipponica*; *Ar*, *Actinidia rufa*; *Euj*, *Eurya japonica*; *Fe*, *Ficus erecta*; *Vb*, *Vaccinium bracteatum*; *Cj*, *Clereya japonica*; *Ps*, *Psychotria serpens*; *Sm* (IM), immature fruits of *Swida macrophylla*; *Tg*, *Ternstroemia gymnanthera*; *Rs*, *Rhus succedanea*; *Ms*, *Myrsine seguinii*; *Dm*, *Diospyros morrisiana*; *C* sp., *Citrus* sp.; *Cc*, *Cinnamomum camphora*; *Elj*, *Elaeocarpus japonicus*; *As* (IM), immature fruits of *Ardisia sieboldii*; *Ns*, *Neolitsea sericea*; and *Ri*, *Rhaphiolepis indica* var. *umbellata.* (Redrawn from Otani and Shibata 2000, with kind permission of Springer)

intact to the total number of seeds ingested. The experiment gave the surprising result that only 4.4% of ingested seeds could pass intact through the macaque gut (Otani 2004). This severe destruction of seeds probably occurred during mastication, because the bite forces of the macaques are overwhelmingly higher (~200 N; Hill et al. 1995) than the pressure resistance of the seeds (9.5 N; Otani 2004), and the macaques do not have mechanical digestive tracts such as the gizzard in birds. The results of another feeding experiment using the fleshy fruits of five species – *Actinidia rufa*, *F. superba* var. *japonica*, *Eurya japonica*, *Eurya emarginata*, and *Vaccinium bracteatum* – showed relatively higher percentages of defecated intact seeds (mean, 23.1%; range, 0–71.2%; Otani, unpublished data) than that of Otani (2004). Seed destruction during foraging behavior by the macaques contrasts significantly with the almost 100% seed passage through frugivorous birds (Yagihashi et al. 1998;

Schabacker and Curio 2000). Seed destruction during foraging behavior can be a major factor in decreasing the effectiveness of seed dispersal by Japanese macaques, and this factor should be examined for other primates and fleshy-fruited plants.

## 6.6 Distance of Seed Dispersal away from Parent Trees

Direction of animal movement away from a fruiting parent tree and distance between a parent tree and seed deposition site have a direct influence on the spatial distribution of seedlings germinated from dispersed seeds. As for seed dispersal via the cheek pouches of Japanese macaques, we can estimate the distance of seed dispersal by closely observing feeding and ranging behavior, assuming that all the spat-out seeds come from the last fruit foraging site or parent tree. Yumoto et al. (1998) and Tsujino and Yumoto (2009) showed the distribution of seed dispersal distance for four fleshy-fruited species with relatively large-sized seeds. For example, seeds of *Persea thunbergii* were carried an average 19.7 m and the maximum distance was 105 m, although more than 80% of seeds were deposited within 30 m from parent trees (Yumoto et al. 1998). Tsujino and Yumoto (2009) also reported a mean seed dispersal distance of several tens of meters (16.7, 26.1, 32.4, and 41.8 m for *Myrica rubra*, *P. thunbergii*, *Litsea acuminata*, and *Neolitsea sericea*, respectively), and illustrated the highly skewed distribution of seed dispersal distance (Fig. 6.3).

In contrast to seed dispersal by spitting out, direct measurement of the distance of seed dispersal by feces has been a near-impossible task, because we cannot trace seeds once they are swallowed by animals. However, a recent development in molecular biology has made it possible to identify the maternal origin of dispersed seeds in fecal samples. Parent trees of seeds in animal feces can be identified by comparing the genotypes between fruiting trees and dispersed seeds (Godoy and Jordano 2001). Terakawa et al. (2009) analyzed the microsatellite loci of *M. rubra*

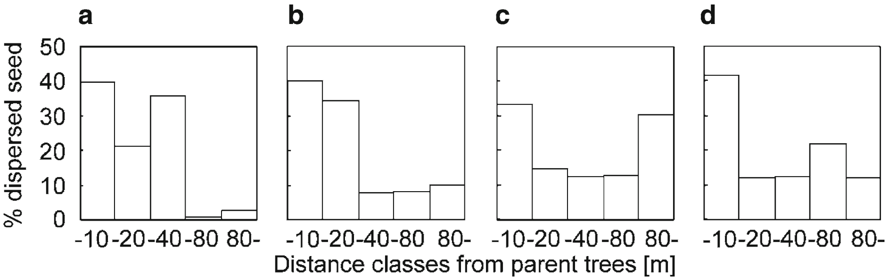

**Fig. 6.3** Percentages of seeds dispersed via cheek pouches of Yakushima macaques at different distances for *Myrica rubra* (**a**), *Persea thunbergii* (**b**), *Neolitsea sericea* (**c**), and *Litsea acuminata* (**d**). (Redrawn from Tsujino and Yumoto 2009, with kind permission of Dr. Tsujino and Wiley-Blackwell)

endocarps dispersed by Yakushima macaques and reported that a fecal sample contained, on average, seeds from three different parent trees, and seed dispersal distance ranged from 20.4 to 634.0 m, with an average of 270.0 m (Fig. 6.4). This is the first estimate of distance of seed dispersal via macaque feces and allows us to discuss the limitations on distance of seed dispersal by Yakushima macaques.

The traveling speed of the macaque groups in the western part of Yakushima was assessed at 2.19 m/min (Maruhashi et al. 1998), and the mean seed retention time in digestive tracts was estimated as 39.1 h by using captive Japanese macaques (Otani 2004). Assuming that the day length is 12.28 h (Agetsuma and Nakagawa 1998) and the macaques are active exclusively in daytime; seeds ingested by the macaques could be transported up to 3,227 m, which is overwhelmingly farther than the seed dispersal distance estimated by Terakawa et al. (2009). In addition, Tsuji et al. (2010) reported that the maximum retention time of seeds and plastic markers in the gut of captive Japanese macaques reached 52–114 h, indicating a potential of extremely longer seed transportation by the macaques. Although the macaques do not travel linearly on the ground, the relative short distance of seed dispersal by feces inferred from the ranging behavior of the Yakushima macaque groups and the small home range (0.29–0.9 km$^2$, Maruhashi et al. 1998; Hanya et al. 2006) limited the expansion of seed deposition sites. Moreover, Japanese macaques shift their foraging site depending on annual and seasonal fluctuations in fruit resources (Agetsuma and Noma 1995; Tsuji and Takatsuki 2008). This observation means that a macaque group tends to use only certain parts of its home range during the foraging period of a major fruit season, implying shorter distances of seed dispersal. In fact, Tsujino and Yumoto (2009) showed that seeds of *M. rubra* and *P. thunbergii*, which grew abundantly on a ridge site, were dispersed primarily

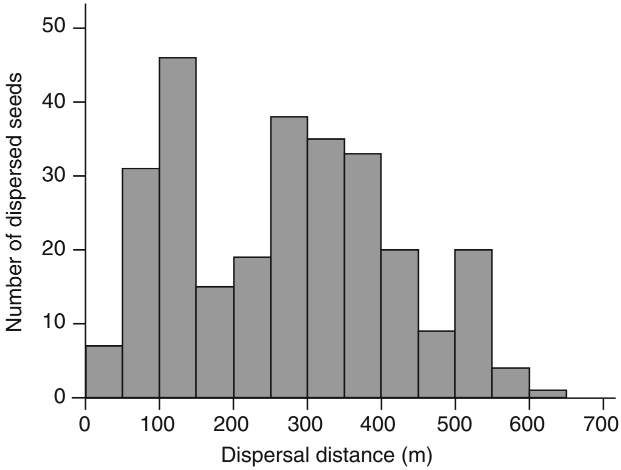

**Fig. 6.4** Number of *Myrica rubra* seeds dispersed by Yakushima macaque feces at different distances. (Redrawn from Terakawa et al. 2009 with kind permission of Dr. Terakawa and Springer)

at the ridge site by spitting behavior; in contrast, seeds of valley growing trees such as *L. acuminata* were deposited at the valley site. These results suggest that the aggregated distribution of parent trees in a specific topography leads to a smaller range of seed deposition, and the location of parent trees is itself a limiting factor for seed deposition.

Yumoto et al. (1998) pointed out that approximately half of *P. thunbergii* seeds removed from parent trees were deposited by spitting on sunny places including road surfaces, when Yakushima macaques rested there. Although a road surface is an unsuitable site for plant recruitment, this fact appears to support the directed dispersal hypothesis that an effective seed disperser deposits seeds on favorable sites for seedling establishment. In the deciduous forests of northern Japan, the home range size of a macaque group is considerably wider (2.3–39.7 km$^2$: Izumiyama et al. 2003; Hanya et al. 2006) than that in the lowlands of Yakushima; thus, seed dispersal distance seems to be longer, yet topography-oriented seed deposition may occur, and a long seed dispersal distance may contribute to enrichment of degraded sites in the northern Japan, because some macaque groups travel over a mosaic of natural and logged forests. If directed dispersal to sunny places or open sites would occur in northern Japan, forest rehabilitation by macaque seed dispersal may enhance degraded sites such as logged forests and abandoned farmlands.

## 6.7 Effects of Macaque Ingestion on Germination

Compared with seeds not ingested by animals, dispersed seeds often exhibit different germination behaviors, such as an increased number of germinated seeds and a shorter period needed for germination (Traveset 1998). Yumoto et al. (1998) found that seeds of three species, *N. sericea*, *P. thunbergii*, and *M. rubra*, that were dispersed by spitting behavior of Yakushima macaques, showed relatively greater germination percentage than seeds collected from trees and defleshed manually, whereas there was no difference between dispersed and nondispersed seeds for *Syzigium buxifolium*. The effects of spitting on germination are not positive for all tree species; this is also applicable in the case of seed dispersal by feces. Otani and Shibata (2000) reported that positive, negative, and neutral effects were observed for seeds defecated by Yakushima macaques, compared with uningested seeds. Unfortunately, these studies of germination traits contained an oversight in experimental design. To compare germination behavior between dispersed and nondispersed seeds, the same seed source must be used for both groups. For example, during a field observation for foraging behavior of the macaques, we can notice that they may choose well-developed and mature fruits that may contain vigorous seeds. If this is true, when a researcher collects control fruits for a germination test from trees that have been foraged by macaques, seed characteristics such as maturity may differ between dispersed and nondispersed seeds.

There is an example of a carefully designed germination test to examine the effects of seed ingestion by macaques. Otani (2004) examined the effects of seed ingestion on germination by using captive Japanese macaques and *E. emarginata* fruits. He found that seeds passed through the macaque gut did not show better germination comparing with that of uningested seeds (Fig. 6.5a,b), although acid- and hot water-bathed seeds showed higher germination percentages than control seeds. The stimulation by gastric acid and body temperature during the gut passage may increase the germination percentage; however, it is inferred that seed ingestion by the macaques also has some negative effects on germination. Otani (2004) also reported that artificially defleshed seeds exhibited higher germination percentages than seeds in intact fruits (Fig. 6.5c,d), implying that the exocarp and the flesh surrounding seeds act as a mechanical or chemical deterrent to germination. These findings suggest that germination enhancement of *E. emarginata* occurs as a

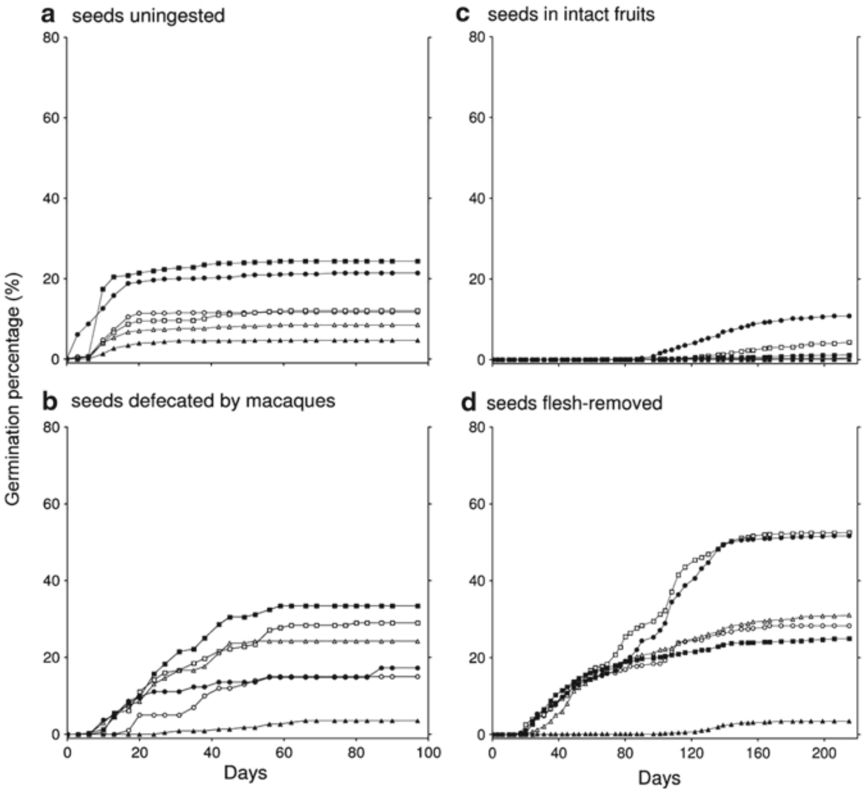

**Fig. 6.5** Germination processes of *E. emarginata* seeds collected from six individual trees: uningested seeds (defleshed seeds) (**a**), seeds defecated by captive macaques (**b**), seeds in intact fruits (**c**), and defleshed seeds (**d**). Comparisons should be made for **a** vs. **b**, and **c** vs. **d**, because seeds of **a** and **d** underwent different treatments. Different symbols correspond to each individual tree. (Redrawn from Otani 2004, with kind permission of Springer)

consequence of flesh removal by foraging, not as a result of gut passage. These results were reported for only one tree species, so more work is needed on other fleshy-fruited species to understand any alterations in germination traits induced by the macaques.

## 6.8 Seed Dispersal and Local Extinction of the Macaque

In evergreen and deciduous forests in Japan, frugivorous birds (e.g., the brown-eared bulbul, *Hypsipetes amaurotis*; the copper pheasant, *Syrmaticus soemmerringii*; the pale thrush, *Turdus pallidus*) and some carnivores (e.g., marten, *Martes melampus*; raccoon dog, *Nyctereutes procyonoides*; Asiatic black bear, *Ursus thibetanus*) also play roles as seed dispersers of fleshy-fruited plants (Otani 2002; Kominami et al. 2003; Koike et al. 2008). Terakawa et al. (2008) pointed out that compared with the common frugivorous bird, the brown-eared bulbul, Yakushima macaques consume approximately 35 times more *M. rubra* fruits in lowland areas of Yakushima (893 fruits/macaque/day vs. 25.1 fruits/bird/day), and the amount of fruit eaten by brown-eared bulbuls did not increase (24.0 fruits/bird/day) even under macaque-free conditions on Tanegashima Island, which is located near Yakushima, where the macaques were extinct in recent times less than 90 years ago. Such a small amount of fruit ingested by bulbuls is probably because of the relatively heavy weight and large size of the *M. rubra* fruits (1.44 g fresh weight, 13.2 mm in diameter; Yumoto et al. 1998). This evidence indicates that bulbuls cannot compensate for the reduction in fruit removal and *M. rubra* seed dispersal in forests without macaques. The Japanese macaque appears to be a reliable seed disperser for arbor trees with large-sized fruits and seeds, although animal contributions to tree recruitment should be compared among more species including birds, macaques, and carnivores.

## 6.9 Future Directions

We still lack general information related to seed dispersal by the macaques in northern Japan, such as seed spitting, seed destruction in the gut, and germination behavior of dispersed seeds. Further research is required to obtain quantified data on seed survivorship through the processes of seed dispersal to fully understand the macaque's contribution to tree recruitment. Comparison of the survival process of seedlings from dispersed and nondispersed seeds should be conducted in both northern and southern Japan. Molecular biological techniques should be applied for more fleshy-fruited species to measure seed dispersal distance directly in evergreen and deciduous forests, where the home range size of a macaque group is widely different. This work may provide a starting point for a discussion on limiting factors of dispersal distance and the macaque's contribution on rehabilitation of degraded forests.

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# Chapter 7: Conservation: Present Status of the Japanese Macaque Population and Its Habitat

**Yasuyuki Muroyama and Aya Yamada**

## 7.1 Introduction

Worldwide, many primate species are in critical danger and threatened with extinction (Chapman and Peres 2001). This is the case for most *Macaca* species. Although macaques are often considered as well known or common, data on their present status including population numbers, distribution, and population trends are insufficient for most species, especially for those that are geographically widespread, such as rhesus (*Macaca mulatta*) and long-tailed (*Macaca fascicularis*) macaques. Available information suggests that most macaque species are experiencing a decline in numbers and/or distribution, although some populations appear to be recovering (Muroyama and Eudey 2004).

Japanese macaques (*Macaca fuscata*) are a well-known species, categorized as lower risk – least concern (LR-lc) in the 2008 IUCN Red List of Threatened Species (Watanabe and Tokita 2008). Their ecology and behavior have been well studied (see other chapters in this volume). However, their population status is poorly understood for most regions of Japan, and their conservation and management have been hampered for various reasons. Japanese macaques, similar to other widespread macaque species, are very adaptable to different environments, from secondary forests to crop fields around human settlements. They thus need appropriate management programs combining conservation and damage management for populations in conflict with local human populations (Muroyama and Eudey 2004; see also Topic 5).

This chapter describes changes in the distribution of Japanese macaques, increasing conflicts between macaques and local people, the ecology and behavior of crop-raiding macaques, and prospects for their conservation and management.

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## 7.2 Changes in the Distribution of Japanese Macaques

Japanese macaques are endemic to the islands of Japan, where they have a somewhat scattered distribution from the Shimokita Peninsula in the north to Yakushima Island in the south (Fig. 7.1a–d). Within this range this species occupies a variety of habitats, including evergreen and deciduous broad-leaved forests

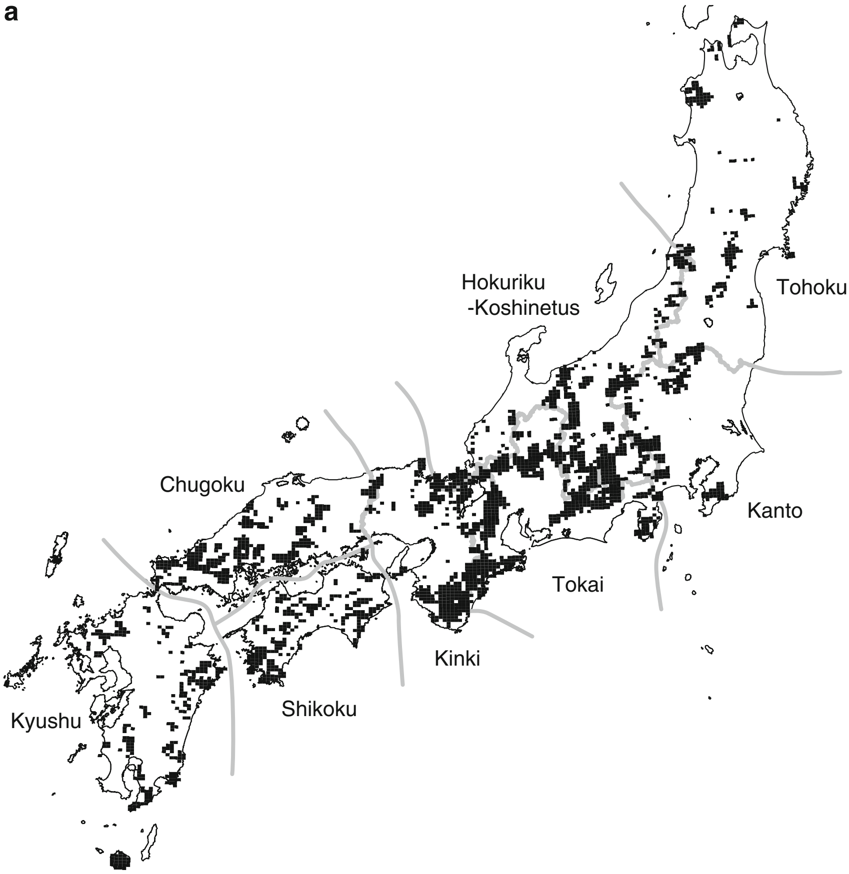

**Fig. 7.1** Distribution of Japanese macaques in 1978 (**a**); in 2003 (**b**); and changes in the distribution between 1978 and 2003 (**c**, **d**): distribution unique to 1978 (**c**), and distribution unique to 2003 (**d**). Tohoku Region includes Aomori, Iwate, Miyagi, Akita, Yamagata, and Fukushima Prefectures; Kanto Region includes Ibaraki, Tochigi, Gunma, Saitama, Chiba, Tokyo, and Kanagawa Prefectures; Hokuriku-Koshinetsu Region includes Niigata, Toyama, Ishikawa, Fukui, Yamanashi, and Nagano Prefectures; Tokai Region includes Gifu, Shizuoka, Aichi, and Mie Prefectures; Kinki Region includes Shiga, Kyoto, Osaka, Hyogo, Nara, and Wakayama Prefectures; Chugoku Region includes Tottori, Shimane, Okayama, Hiroshima, and Yamaguchi Prefectures; Shikoku Region includes Tokushima, Kagawa, Ehime, and Kochi Prefectures; Kyushu Region includes Fukuoka, Saga, Nagasaki, Kumamoto, Oita, Miyazaki, and Kagoshima Prefectures. (Data from Biodiversity Center of Japan, Ministry of the Environment, Japan 2004)

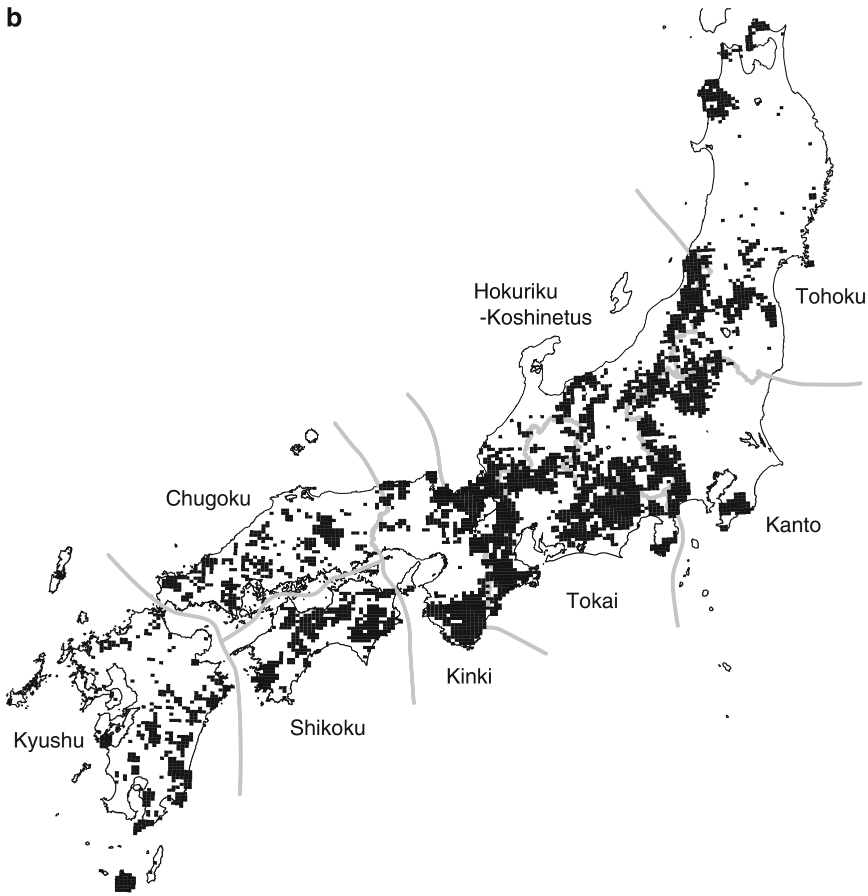

**Fig. 7.1** (continued)

and alpine zones (see Chap. 4). However, the present distribution of Japanese macaques has been and is limited by human activities such as habitat degradation and loss resulting from the expansion of human settlement, hunting for food and traditional medicine, and capture as agricultural pests (Sprague 2002; Muroyama and Eudey 2004). Japanese macaques can thrive in secondary forests around human settlements; consequently, conflicts between macaques and local people are inevitable, and most arise over crop-raiding.

### *7.2.1 Before World War II*

The distribution of Japanese macaques has been affected by human activities for centuries but has varied drastically in recent decades. Before World War II,

**Fig. 7.1** (continued)

Japanese people utilized timber and nontimber forest resources intensively. Timber resources were used for architecture and fuel, and nontimber resources such as various plant materials (fruits, acorn, nuts, leaves, and grasses) and animal materials (skins, feathers, and meat) were used for food, medicine, agricultural fertilizers, and various other day-to-day uses (e.g., clothing or decoration; Sprague 2002). Intensive use, or overuse, of forest resources around villages combined with rapid human population growth caused habitat loss for Japanese macaques and other wildlife in the plains areas of Japan (Ogura 1992; Tsunekawa and Bessho 2001). Even in some of the mountainous areas, use of vast amounts of fuel wood for pottery or mineral refinement changed forest to grassland or bare mountains (Chiba 1991; see also Topic 4 for details).

In rural parts of Japan, macaques were hunted for their meat and for medicinal uses. The hunting pressure on macaques probably became heavier after the establishment of a new government under Emperor Meiji, when prohibitions against farmers or commoners owning firearms were lifted. As a result, inexpensive Japanese-made

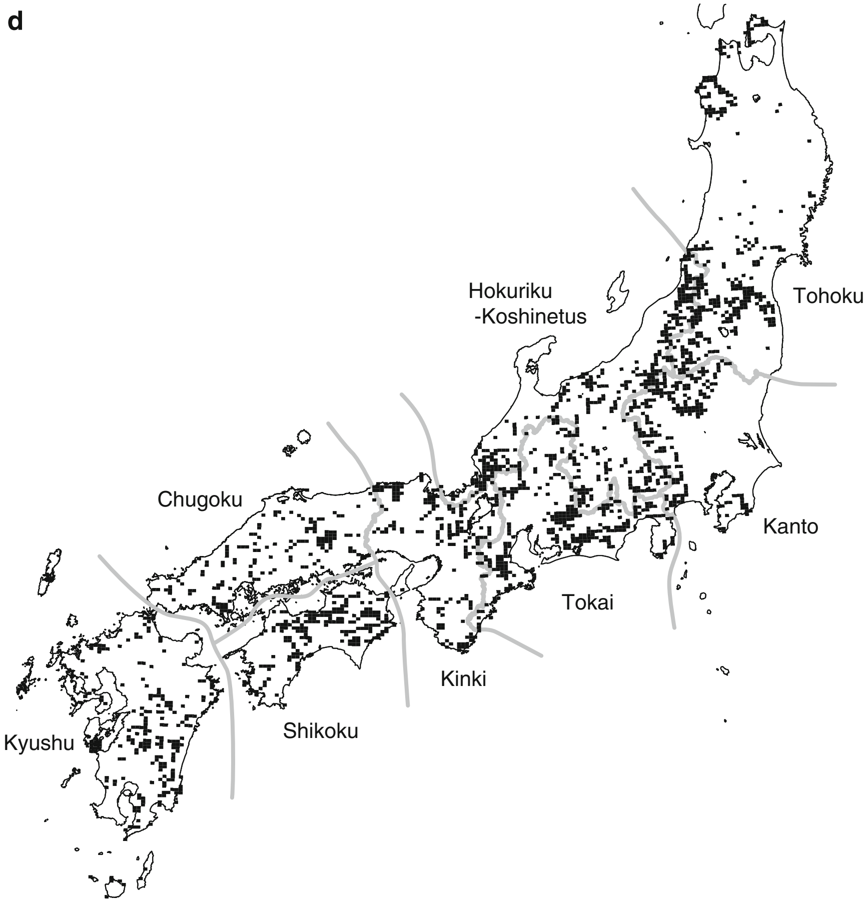

**Fig. 7.1** (continued)

rifles became readily available, and the commercial hunting of macaques expanded (Hanai 1995; Mito and Watanabe 1999; Sprague 2002). Hunting is likely to have exterminated macaques from much of their range in northeastern Honshu Island (Mito 1992; Mito and Watanabe 1999). Continuous habitat loss caused by human encroachment and hunting for food and medicine removed macaques from forests around villages, and thus the distribution of Japanese macaques continued to decline until at least the end of World War II (Mito and Watanabe 1999).

### *7.2.2 After World War II and the "Fuel Revolution"*

As the macaque population was estimated to have suffered a serious decline, hunting regulations to protect macaques from commercial and sport hunting were introduced in 1947. The use of macaques as a natural resource for their meat and for medicine thus ceased (Hirose 1979; Mito and Watanabe 1999). Consequently, one of the most serious threats to the Japanese macaque populations was removed at this time.

Nonetheless, in the late 1950s large-scale habitat degradation and loss for Japanese macaques started anew all over Japan. A policy of "expansive afforestation" was introduced, replacing existing broad-leaved forests with single-species stands of commercially important conifer species such as Japanese cedar (*Cryptomeria japonica*), Japanese cypress (hinoki; *Chamaecyparis obtusa*), and Japanese larch (*Larix kaempferi*). Between 1960 and 1971, some 3,000 km$^2$ of broad-leaved forests were replaced by conifer plantations each year. These plantations occupied large areas within macaque habitats and diminished the quality of macaque habitats because Japanese macaques depend primarily on the fruits, seeds, flowers, and new and mature leaves of broadleaf flora for food (Agetsuma and Nakagawa 1998). Although the amount of conifer plantation replacing broad-leaved forests has decreased gradually each year, it occupied 41% (103,467 km$^2$) of forest areas in Japan (250,970 km$^2$) in 2007 (Forestry Agency, Japan 2007).

Most forms of traditional forest resource utilization practiced by Japanese people for centuries continued for a while after the end of the World War II. However, in the 1950–1960s the "fuel revolution" occurred and petroleum fuels replaced charcoal, firewood, and dried leaves as the most commonly used fuels. Consequently, charcoal production drastically decreased from 2,089,000 tons to 35,000 tons from 1955 to 1980 (Forestry Agency, Japan 1963, 1982). The fuel revolution was accompanied by a fertilizer revolution, as chemical fertilizers replaced green fertilizers such as leaves and grasses provided from forests. Thus, the intensive forest utilization on which agriculture and daily life had depended ceased, and the numbers of people working in forests around villages decreased drastically (Tsunekawa 2001). In this manner, rural communities lost the buffer zone of human activity (Sprague 2002), or human pressure (Muroyama 2003; Muroyama and Suzuki 2007), that protected crop fields from damage by wildlife, and the border created by human activity between crop fields and wildlife habitats moved from the deep mountains to the forests immediately around human settlements (Muroyama 2003; Muroyama and Suzuki 2007). In addition, as a consequence of a general change in economic structure the human population declined and aged and no longer had the manpower or sufficient money to pay for protection from wildlife. These sociological changes made the secondary forests around villages an appropriate habitat for Japanese macaques.

### 7.2.3 Changes in the Distribution of Japanese Macaques Between 1978 and 2003

With changes in hunting pressure and habitat conditions in recent decades, the distribution of Japanese macaques has been expanding, although regional differences in the status of local populations have been found (Watanabe 2000; for details of the changes estimated by questionnaire surveys, see Watanabe and Muroyama 2005). According to the National Survey of the Biodiversity Center of Japan,

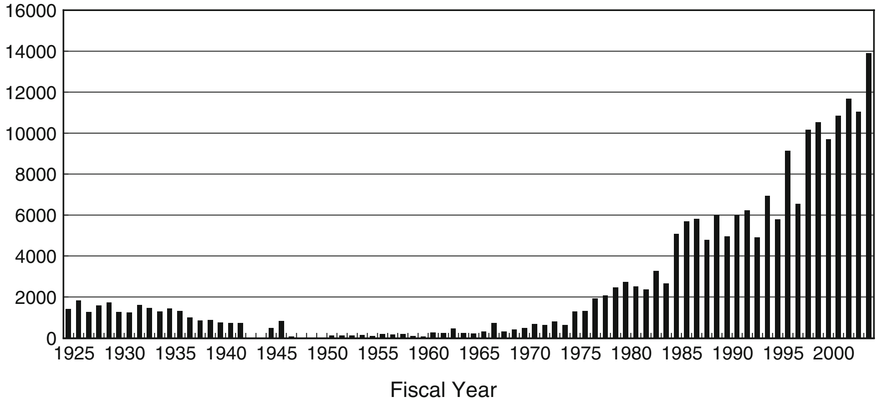

**Fig. 7.2** Number of Japanese macaques removed by hunting (up to 1948) and captured as nuisance animals (after 1948) or as subjects of population control under the Specified Wildlife Conservation and Management Plan (after 2001). [Data from Shuryo Tohkei (Forestry Agency 1925–1971) and Choju Kankei Tohkei (Ministry of the Environment 1972–2005)]

Ministry of the Environment (2004), the number of 5 × 5 km cells containing monkey groups increased from 2,284 in 1978 to 3,471 in 2003 (Fig. 7.1a, 1978; Fig. 7.1b, 2003; Fig. 7.1c, unique to 1978; Fig. 7.1d, unique to 2003). The distribution has expanded rapidly and the population has possibly recovered in northeastern regions of Japan such as Tohoku, and Kanto, Hokuriku-Koshinetsu, and Tokai Regions, where local populations had previously been fragmented and locally exterminated by strong hunting pressure. In contrast, in southwestern Japan (Kinki, Chugoku, Shikoku, and Kyushu Regions), the expansion of macaque distribution to village peripheries and the local extinction and fragmentation of populations as a result of culling as an agricultural pest have occurred simultaneously (see also Fig. 7.2). Muroyama et al. (1999) reported a shift and/or diffusion of macaque distribution from the interior to the edge of forests and that macaque groups disappeared from the center of the Kii Peninsula of Kinki Region between 1978 and 1998, where most of the forests now consist of conifer plantation.

However, the survey results may not be very reliable, as the data were obtained from interviews with a limited number of individuals. It is also unclear whether the expanded distribution really indicates a growing population, as conifer plantations have increasingly replaced broad-leaved forests, possibly reducing macaque population density (Takasaki 1981a,b).

## 7.3 Increase of Agricultural Depredation by Macaques

As the macaque distribution around human settlements increased, crop-raiding by macaques occurred in some areas, and culling of macaques as agricultural pests began. The number of macaques culled annually has increased gradually and exceeded 2,000 per year for the first time in 1978 (Fig. 7.2).

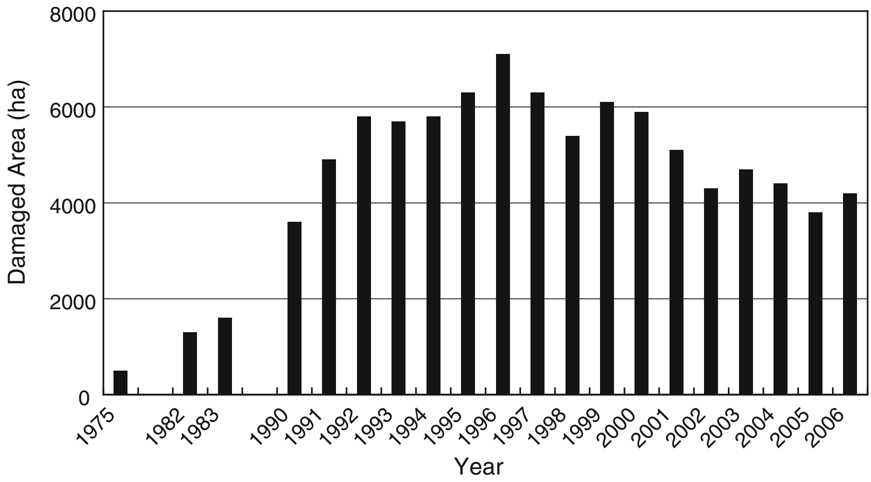

**Fig. 7.3** Area of agricultural damage caused by Japanese macaques in Japan. [Data from Zenkoku no Yaseichoju ni yoru Nosakumotsu Higaijokyo (Ministry of Agriculture, Forestry, and Fisheries 1975–2006)]

Crop damage continued to increase through the 1980s and into the early 1990s (Fig. 7.3). By the late 1980s, crop-raiding by macaques had been reported from all over Japan (Watanabe 2000; Oi and Masui 2002). The area damaged by macaques reached some 6,000 ha in 1992 and remained at this level until 2000. Since 2000, the damaged area has apparently decreased gradually to around 4,000 ha by the late 2000s. However, these results are misleading because the area of abandoned crop fields, partly caused by wildlife-induced agricultural damage, has increased since 1985 (Ministry of Agriculture, Forestry, and Fisheries, Japan 2005).

The change in crop damage in the past two decades differs between regions (Fig. 7.4). The damaged area has decreased gradually but with large variations in all regions, except for Tohoku Region, where it appears to have increased slightly, partly because the recent, rapid expansion of macaque distribution has led to crop-raiding in areas where people have not had to defend their land against macaques for many decades and thus are inexperienced.

As the area of crop damage has increased, the number of macaques culled as agricultural pests has increased rapidly. The number of macaques culled annually has been 10,000 on average since 1998 (see Fig. 7.2). Culling has increased in some regions such as Tohoku, Hokuriku-Koshinetsu, Shikoku, and Kyushu between 1998 and 2004, whereas other regions such as Kanto, Tokai, Kinki, and Chugoku showed no clear tendency (Fig. 7.5). Little correlation between the area damaged by macaques and the number of macaques culled has been found. Damage management for macaque crop-raiding currently relies on culling irrespective of the actual effect of removing macaques in alleviating crop damage.

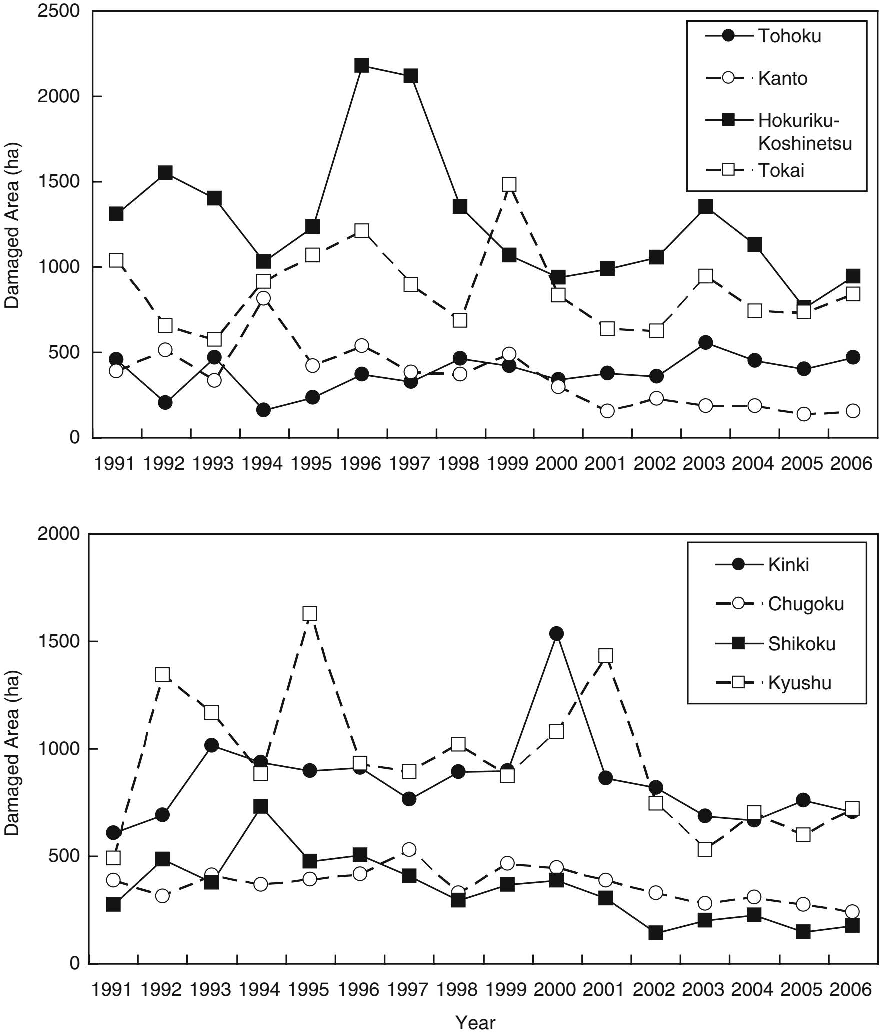

**Fig. 7.4** Changes in the area of agricultural damage caused by Japanese macaques for each region of Japan from 1991 to 2006. [Data from Zenkoku no Yaseichoju ni yoru Nosakumotsu Higaijokyo (Ministry of Agriculture, Forestry, and Fisheries 1975–2006).] See legend of Fig. 7.1 for prefectures included in each region

## 7.4 Ecology and Behavior of Crop-Raiding Japanese Macaques

Groups of Japanese macaques have relatively stable home ranges and make no long migrations, apart from macaques inhabiting alpine zones (Izumiyama 2002). Reproductive parameters vary with annual variation of both biotic factors (e.g.,

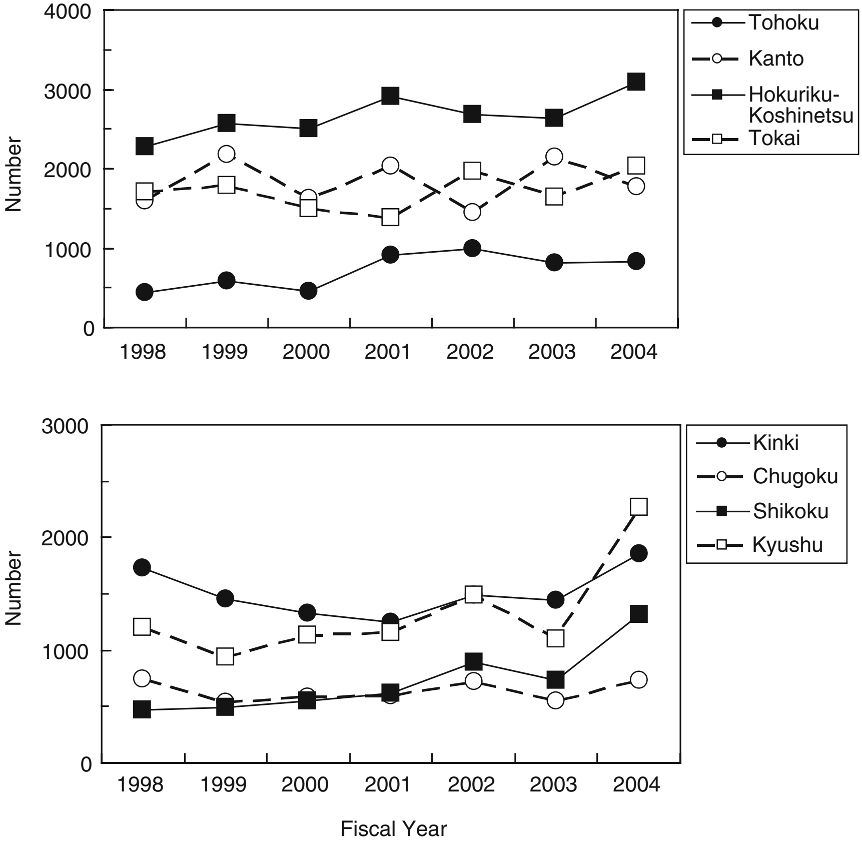

**Fig. 7.5** Number of Japanese macaques captured as nuisance animals or as subjects of population control under the Specified Wildlife Conservation and Management Plan in each region of Japan from 1998 to 2004. [Data from Choju Kankei Tohkei (Ministry of the Environment 1972–2005).] See legend of Fig. 7.1 for prefectures included in each region

food resources) and abiotic factors (e.g., snowfall, temperature) (Izawa 1988; Suzuki et al. 1998; Hanya et al. 2004), but population density is limited by the carrying capacity of the habitat (see Chap. 4). Population size remains stable over long periods of time in populations where macaque distribution is limited (Izumiyama 2002), or else population size grows slowly at the rate of 4.7–5.6% (Nakayama 2002; Taroda-Takizawa 2002).

Macaques seem to change their ecology and behavior after they begin to use crop fields as feeding sites (Muroyama 2003). Our current understanding of changes in food repertoire, reproductive parameters, home range size, habitat use, and behavior toward humans is described next.

### 7.4.1 Food Repertoire

The food repertoire of Japanese macaques is acquired through learning (Ueno 2005; Tarnaud and Yamagiwa 2008). Thus, any plant or animal materials that macaques do not recognize as food are not fed on by them. At the initial stage of crop-raiding, macaques start to feed on the fruits of persimmon and chestnut in villages (for photograph, see Fig. 17.9b), which grow naturally in the forests around human settlements, whereas most of the agricultural crops and fruits, unfamiliar to macaques (for photographs, see Figs. 17.1, 17.9a), are not recognized as food and remain undamaged. As macaques become habituated to humans and the human-related environment, they are more likely to have opportunities to access crop fields and to examine whether each kind of crop or fruit is edible. They may try feeding on various kinds of crop foods and thus widen their food repertoire. Given the opportunity to learn, the macaques will eat any agricultural products and plant materials found in villages, apart from those that are too hot or too bitter (Muroyama 2003).

### 7.4.2 Reproductive Parameters

The value of crop foods for macaques is assumed to be higher than that of wild foods in terms of digestibility, foraging efficiency and nutritional content. Human crop foods are generally lower in fiber than wild foods (see Forthman-Quick and Demment 1988), which makes them a more readily digestible source of energy. Individual items of crop food are also typically larger than most natural food items, which increases foraging efficiency. In addition, the distribution of crop fields is likely to be more clumped than that of natural food sources, which may enable monkeys to reduce the costs of searching for, and moving between, food patches (Forthman-Quick 1986; Altmann and Muruthi 1988; Saj et al. 2001). Consequently, use of crop foods is likely to provide good nutritional conditions for monkeys and lead to a high birth rate and low infant mortality.

Recent studies on crop-raiding groups confirm this hypothesis (Table 7.1, Fig. 7.6). Birth rates of provisioned and crop-raiding groups are much higher than those of groups that do not raid crops (provisioned, 0.50–0.62; crop-raiding, 0.48–0.70; no crop-raiding, 0.27–0.38). Infant mortality appear to be lower, and age at first birth appears to be slightly lower, in crop-raiding groups, as it is in provisioned groups, when compared with groups that do not raid crops. Nevertheless, data on crop-raiding groups are limited.

High birth rate, low infant mortality, and early first birth result in growth of local macaque populations in those agricultural areas suffering from crop damage by macaques. Once crop-raiding groups reach a large population size, they may split into two smaller groups, and one or both groups may start to move into new areas, leading to an escalation in damage at the edges of macaque distribution and a pattern of ongoing encroachment. This pattern seems to have happened in many areas damaged by macaques (Muroyama 2003).

**Table 7.1** Reproductive parameters of Japanese macaques in different study sites

| | Study site | Vegetation type | Birth rate | Mortality of newborns | Age at first birth (year) | |
|---|---|---|---|---|---|---|
| Wild group (group with no crop-raiding) | Kinkazan | Deciduous forest | 0.35 | 0.23 | 7.1 | Takahata et al. (1998) |
| | Kinkazan | Deciduous forest | 0.38 | 0.37 | – | Calculated from Izawa (1990) |
| | Hakusan | Deciduous forest | – | 0.32 | | Calculated from Taroda-Takizawa (2002) |
| | Nikko | Deciduous forest | 0.33–0.34 | – | – | Koganezawa (2002) |
| | Shiga Heights | Deciduous forest | 0.35 | 0.53 | – | Suzuki et al. (1975) |
| | Ryozen | Deciduous forest | 0.34 | 0.28 | 6.7 | Sugiyama and Ohsawa (1982) |
| | Yakushima | Evergreen forest | 0.27 | 0.25 | 6.1 | Takahata et al. (1998) |
| Provisioned group | Ryozen | Deciduous forest | 0.59 | 0.15 | 5.2 | Sugiyama and Ohsawa (1982) |
| | Arashiyama | Deciduous forest | 0.54 | 0.10 | 5.4 | Koyama et al. (1992) |
| | Katsuyama | Deciduous forest | 0.50 | 0.10 | 5.4 | Itoigawa et al. (1992) |
| | Koshima | Evergreen forest | 0.62 | 0.19 | 6.0 | Watanabe et al. (1992) |
| Crop-raiding group | Shimokita | Deciduous forest | 0.50 | – | – | Suzuki (unpublished) |
| | Shimokita | Deciduous forest | 0.48–0.65 | 0.08–0.16 | 5.6 | Nakayama (2002) |
| | Nukata | Deciduous forest | 0.52 | – | – | Calculated from Aichi Prefecture (1994) |
| | Murou | Deciduous forest | 0.55 | – | – | Yamada (unpublished data) |
| | Ooyamada | Deciduous forest | 0.53–0.70 | – | – | Muroyama (unpublished data) |

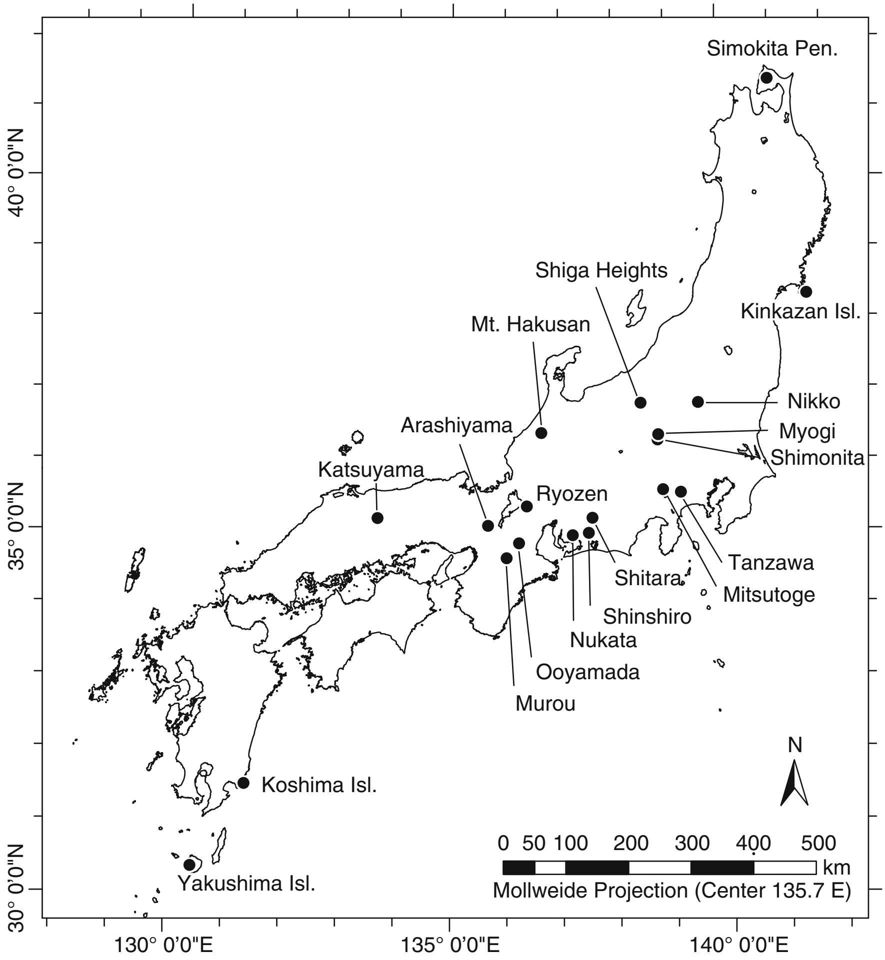

**Fig. 7.6** Locations of study sites mentioned in the present chapter. [The base map is originated from "Boundary data of cities, towns and villages of Japan ver. 6.2" by ESRI Japan Corporation, with permission]

## *7.4.3 Home Range Size*

Broad-leaved forests provide macaques with various kinds of food resources and thus the amount of broad-leaved forest in the home range may limit the number of macaques living there. Previous studies have found that home range size per animal was 8–24 ha in deciduous broad-leaved forests of the cool-temperate zone (possibly lower-quality habitat) and 1.4–1.7 ha in evergreen broad-leaved forests of the warm-temperate or subtropical zone (possibly higher-quality habitat; Takasaki 1981a; see also Chap. 4). Furuichi et al. (1982) also reported that macaque groups living in the habitats including low-quality forests such as conifer plantations had a larger home range size per animal, whereas the home range size per animal for groups in broad-leaved forests was similar to that of groups living in undisturbed habitat. Thus, group size is correlated to the area of broad-leaved forest within the home range, rather than the home range size per se. Further complexity may be added because the availability and abundance of food resources varies with the plant species composition of broad-leaved forests.

Table 7.2 lists the home range size and home range size per animal of crop-raiding groups at different study sites. Home range size per animal for all habitat types ranged from 6.1 to 73.1 ha. However, for 9 of the 16 groups, the area of broad-leaved deciduous forest per animal was 8–24 ha, as reported by Takasaki (1981a). Most groups with access to a greater area of cropland (nos. 6–12) had smaller areas of broad-leaved forest per animal than groups with access to small areas of cropland within their home range (nos. 2–5). This observation may indicate that the use of crop fields results in more effective foraging for the macaques such that a smaller home range size is required, as suggested by Izumiyama et al. (2003).

### 7.4.4 Habitat Use

Previous studies have reported that in general crop-raiding groups prefer evergreen and deciduous broad-leaved forests as foraging sites and avoid conifer plantations (Yamada 2004; Imaki et al. 2006; Nagata et al. 2007). Broad-leaved forests are recorded as used frequently throughout the year (Imaki et al. 2006) or during spring and autumn (Yamada 2004; Nagata et al. 2007). In contrast, macaques have been found to avoid conifer plantations in some study sites (Murou: Yamada 2004; Tanzawa: Nagata et al. 2007), although they show no avoidance/preference toward conifer plantations at other sites (Nikko: Imaki et al. 2006). These regional variations may result from relative differences in the importance of broad-leaved forests for food resource and/or that of conifer plantation for cover.

Crop-raiding may or may not vary seasonally. Thus, macaques may exhibit a preference for crop fields only during winter (Nagata et al. 2007), from spring to autumn (Imaki et al. 2006), or throughout the year (Yamada 2004) depending on the location of the study. Whether or not monkeys use crop fields is determined by the quality and availability of both crop foods and wild foods (Muroyama 2003, 2005). For instance, monkeys are more likely to raid crop fields when wild foods become scarce and/or their quality becomes lower, even if the availability of crops remains the same (Naughton-Treves et al. 1998; Siex and Struhsaker 1999). Regional variations in food resource condition in different seasons may result in seasonal differences in crop-raiding by macaques.

Forests around human settlements including forest edges, irrespective of actual vegetation types, are also reported to be used frequently (Yamada 2004; Imaki et al. 2006). Such forests may be a place where macaques stay and watch for opportunities for crop-raiding in the absence of humans, or may consist of secondary vegetation types that provide food for macaques.

**Table 7.2** Home range size and per-animal range area size of crop-raiding groups in different study sites

| | | | | Range size ($km^2$) | | | Home range size per animal (ha) | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| No. | Study site | Vegetation type | Group size | All habitat types | Broad-leaved forest | Cropland | All habitat types | Broad-leaved forest | Methods | Source |
| 1 | Shimokita | Deciduous forest | 60 | 30.7 | 13.0 | 2.0 | 51.2 | 21.7 | MCP (100%) | Suzuki (unpublished data) |
| 2 | Nikko | Deciduous forest | 32 | 5.9 | 4.7 | 0.0 | 18.4 | 14.6 | AK (95%) | Imaki et al. (2000) |
| 3 | Nikko | Deciduous forest | 44 | 7.7 | 6.1 | 0.0 | 17.7 | 14.1 | AK (95%) | Imaki et al. (2000) |
| 4 | Nikko | Deciduous forest | 27 | 10.9 | 3.7 | 0.0 | 41.1 | 14.1 | AK (95%) | Imaki et al. (2000) |
| 5 | Nikko | Deciduous forest | 68 | 26.8 | 8.4 | 0.3 | 39.7 | 12.4 | AK (95%) | Imaki et al. (2000) |
| 6 | Nikko | Deciduous forest | 79 | 20.7 | 4.8 | 1.8 | 26.2 | 6.1 | AK (95%) | Imaki et al. (2000) |
| 7 | Nikko | Deciduous forest | 45 | 13.3 | 1.8 | 2.3 | 29.6 | 3.9 | AK (95%) | Imaki et al. (2000) |
| 8 | Tanzawa | Deciduous forest | 80 | 10.9 | 4.8 | 0.9 | 13.6 | 6.0 | 250 m grid | Nagata et al. (2007) |
| 9 | Tanzawa | Deciduous forest | 71 | 11.7 | 4.0 | 1.4 | 16.5 | 5.6 | 250 m grid | Nagata et al. (2007) |
| 10 | Tanzawa | Deciduous forest | 70 | 15.1 | 3.8 | 1.3 | 21.6 | 5.4 | 250 m grid | Nagata et al. (2007) |
| 11 | Mitsutouge | Deciduous forest | 87 | 11.0 | 1.4 | 1.5 | 12.6 | 1.6 | MCP (95%) | Yamanashi Prefecture (2001) |
| 12 | Mitsutouge | Deciduous forest | 72 | 4.4 | 0.9 | 0.6 | 6.1 | 1.3 | MCP (95%) | Yamanashi Prefecture (2001) |
| 13 | Nukata | Deciduous forest | 35 | 25.6 | 6.7 | – | 73.1 | 19.0 | MCP (100%) | Aichi Prefecture (1994) |
| 14 | Shitara | Deciduous forest | 28 | 19.5 | 4.4 | – | 69.6 | 15.7 | MCP (100%) | Aichi Prefecture (1994) |
| 15 | Shinshiro | Deciduous forest | 47 | 31.5 | 5.7 | – | 67.0 | 12.2 | MCP (100%) | Aichi Prefecture (1994) |
| 16 | Murou | Deciduous forest | 55 | 39.7 | 5.8 | 2.3 | 72.2 | 10.5 | MCP (100%) | Yamada (unpublished data) |
| 17 | Ooyamada | Deciduous forest | 73 | 18.8 | – | – | 25.8 | – | MCP (100%) | Muroyama (unpublished data) |
| 18 | Ooyamada | Deciduous forest | 44 | 26.4 | – | – | 60.0 | – | MCP (100%) | Muroyama (unpublished data) |

MCP, minimum convex polygon; AK, adaptive kernel

The home range size of crop-raiding groups seems to be relatively stable, as found for non-crop-raiding groups; however, one case has been reported of a group ranging far out of the original home range (Hanya et al. 2002). Whether such behavior is characteristic of crop-raiding groups remains unclear.

### *7.4.5 Behavior Toward Humans*

As macaques visit crop fields in villages and encounter local people with more frequency, they gradually habituate to people and the human-related environment and lose their fear and cautiousness in this situation. Consequently, macaques start to feed on crops in fields even when farmers are working nearby and to rest on the roofs of houses. In more extreme cases, macaques enter houses through unlocked doors or windows to eat something and may threaten young and elderly people.

Macaques habituated to humans cause nuisance and psychological damage through disturbance of daily life with their noise and droppings and the fear of their threatening behavior or the potential of being attacked by them. These concerns can become a serious problem in some areas.

### *7.4.6 Consequences of Crop-Raiding*

High birth rate and low infant mortality in crop-raiding groups has resulted in growth of local macaque populations in agricultural areas. The subsequent encroachment of macaques into areas where they have not previously lived has led to escalating damage along the edges of the macaque distribution and a pattern of continuing encroachment. Furthermore, these macaques are more likely to depend on crops, fruits, and other food resources in villages. This negative feedback pattern has occurred all over Japan.

Unfortunately, there are few studies on the ecology and behavior of crop-raiding macaques, particularly with respect to habitat use for human-related environments such as villages, farmlands, and forests around human settlements. To ensure the long-term conservation of this species, further studies are required.

## 7.5 The Present Status of and Prospects for Conservation and Management of Japanese Macaques

The increased distribution of Japanese macaques and increasing agricultural damage of recent decades, as well as the associated changes in their ecology and behavior, has cast a bleak shadow over the future of this species. The recovery of macaque distribution and the population from the reduced population at the end of World War II should be welcomed for the conservation for Japanese macaques. However, many macaques have been culled as troublesome pest animals, and some local populations have become extinct, particularly in southwestern Japan. The present status and prospects for conservation and management for Japanese macaques are briefly reviewed next.

### *7.5.1 Present Status*

For the conservation and management of wildlife in Japan, The Ministry of the Environment (2007) issues a document entitled "Basic Guidelines for Implementing Wildlife Management Projects." The guidelines are based on the Wildlife Protection and Proper Hunting Law (revised in 1999), which included the concept of scientific and systematic wildlife conservation and management for the first time in Japan. According to the guidelines, prefectural governments, which are mainly responsible for wildlife conservation and management, must plan and implement wildlife projects including all issues concerning hunting and management, such as the capture and removal of wildlife and bird eggs and designating wildlife protection areas. The projects also include a legally defined type of scientific management plan for wildlife, called the Specified Wildlife Conservation and Management Plan (SWCMP).

The SWCMP aims to conserve wildlife populations appropriately and to alleviate human–wildlife conflicts by using three kinds of management: population management, habitat management, and damage management. The SWCMP provides a legal base to promote a scientific and systematic wildlife management program, but prefectural governments are not obliged to adopt it for all wildlife. Consequently, of the 44 prefectures that Japanese macaques inhabit, only 19 prefectures had planned and implemented the SWCMP for macaques by 2009. Moreover, many of these plans have produced unsatisfactory results for the control of conflicts between macaques and local people, partly because few local governments have adequate systems and personnel numbers to plan and implement appropriate management programs based on scientific data.

Many researchers have stated that culling of crop-raiding macaques with no appropriate management program has proved to be ineffective for the reduction of crop damage (e.g. Muroyama 2003). Nevertheless, in Japan, many macaques have still been removed as agricultural pests and/or as a nuisance with permits issued under the nuisance animal provisions, without any implementation of SWCMP or scientific monitoring of the status of the population or the damage caused.

### *7.5.2 Prospects for Conservation and Management of Japanese Macaques*

#### 7.5.2.1 Damage Management

Feeding on human crop foods by macaques has resulted in the rapid growth of macaque populations and the expansion of macaque distribution around human settlements with a pattern of increasing crop damage. A first action must therefore be to reduce the opportunity for macaques to feed in villages, and thereby to lower the macaques' dependency on crop foods (Muroyama 2005). For this purpose, community-based management projects to combat macaque crop-raiding need to be encouraged, with financial and technical support from local government and related organizations (see also Topic 5).

The most important principle for damage management is to reduce available food resources in villages, such as crops and harvested fruits, as well as garbage, vegetable refuse, and unharvested fruits (Inoue 2002; Muroyama 2003, 2005). A variety of countermeasures including physical and psychological barriers against macaques are also useful. Appropriate techniques should be selected on the basis of economy, feasibility, and the ease of use and maintenance by elderly local people, as well as the effectiveness for target species. Recently, The Ministry of Agriculture, Forestry and Fisheries issued Basic and Practical Manuals for Crop Damage by Wildlife (2006, 2007) to promote damage management by local communities.

#### 7.5.2.2 Population Management

To control the expanding population of crop-raiding macaques but avoid local extinction, population management data from scientific monitoring are required. Unfortunately, although macaques have been culled as agricultural pests or for population control without appropriate management plans in place for several decades, there are few data on the effects of this culling in terms of damage reduction or control of the expanding population.

Recently, some local governments have initiated population management plans based on scientific management plans including monitoring (e.g., Murou, Nara Prefecture; Simonita, Myogi, Gunma Prefecture). These measures have been designed to control population expansion, changes in home ranges and the area damaged. However, many more case studies of population management based on management plans with scientific data are needed. Because population management in damaged areas is of prime importance, studies of population management in these areas are of particular importance for the appropriate conservation and management of Japanese macaques. Such studies need to determine probable measures for controlling population expansion and limiting the damage caused without risk of local extinction.

#### 7.5.2.3 Habitat Management

As mentioned earlier, the expansion of conifer plantations, which started in the late 1950s, has markedly degraded the quality of wildlife habitat. Conifer plantations have replaced and thus reduced the area of broad-leaved forest, the appropriate habitat for most Japanese mammals. Although we have no data describing the effects of this drastic environmental change on populations of Japanese macaques, areas of intensive conifer afforestation may have become an inappropriate habitat for this species. Restoration of or recovery from conifer plantation to broad-leaved or mixed forests may be one means of habitat management to conserve local populations of macaques living in habitats dominated by conifer plantations. To evaluate the possible effects of such restoration, synthetic analyses of local populations involving several macaque groups are required. Moreover, for these analyses to be accurate in the long term, basic ecological monitoring data (food habits, habitat use, population parameters, vegetation parameters, geography, and so on) should ideally be available for these groups. The ecology of other wildlife (e.g., sika deer) living in the restoration area must also be taken into consideration because restoration of the area may incur short- or long-term negative effects on these species.

Secondary forests around villages (i.e., “Satoyama” in Japanese) are another candidate for habitat management. This type of forest has become a popular target for conservation activities for secondary flora and fauna (Hattori et al. 1995). Conservation activities in “Satoyama” can have a variety of purposes. One of them may be to reconstruct psychological boundaries between human settlements and wildlife habitats, to control the expansion of macaque distribution. Frequent use of forests around villages may reconstruct the buffer zone of human activity, lost in the 1960s when forest utilization for timber and nontimber resources ceased (Sprague 2002). To promote forest utilization, other kinds of resources, such as ecological, cultural, and educational resources, need to be explored (Hattori et al. 1995; Kameyama 1996).

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# Part III

# Intra-specific Variation: Behaviors and Social Relationships

# Chapter 8: The Ecological Design of the Affiliative Vocal Communication Style in Wild Japanese Macaques: Behavioral Adjustments to Social Contexts and Environments

**Hiroki Koda and Hideki Sugiura**

## 8.1 Introduction: Contact Calls in Primates Serve to Maintain Group Spatial Cohesion

Vocal communications are essential in nonhuman primates because primates are usually organized into a wide variety of social groups (Smuts et al. 1987). Early studies on primate vocalizations focused primarily on classifying vocalizations into a sound spectrogram, including classifications of the calls of Japanese macaques (*Macaca fuscata*; Green 1975) and rhesus macaques (*Macaca mulatta*; Rowell and Hinde 1962). Because the playback experiment offers a simple and practical method for studying vocal communication in the wild, many empirical studies have used this approach (Seyfarth and Cheney 1990; Cheney and Seyfarth 2007). The cognitive and functional aspects of alarm calls have been particularly central topics in the domain of vocal communication (Zuberbuhler 2003; Arnold and Zuberbuhler 2006). Many studies have provided interesting evidence for the vocal flexibility and referential meanings of primate alarm calls. However, the vocal signals in alarm calls tend to be conservative or innately programmed in terms of vocal features and general usage because these calls advertise the presence of predators and have greater survival value than do other affiliative calls (Elowson and Snowdon 1994; Snowdon and Hausberger 1997; Snowdon and Elowson 1999). Indeed, vocal flexibility or variation has evolved in affiliative rather than in alarm calls (Oller and Griebel 2008). In this chapter, we focus on the variability or flexibility in affiliative calls (i.e., contact calls).

Many social animals including primates use contact calls. Primates are usually organized into a wide variety of social groups in which the behaviors of members are coordinated. In nonhuman primate social groups, contact calls serve to maintain

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interindividual spatial cohesion more efficiently than does visual contact (i.e., monitoring of group members; for review, see Boinski and Garber 2000). Several studies have shown that adult monkeys frequently produced contact calls to prevent separation from other group members [Japanese macaques: Itani 1963; rhesus macaques: Rendall et al. 1996; chacma baboons (*Papio cynocephalus ursinus*): Cheney et al. 1996; Rendall et al. 2000; white-faced capuchins (*Cebus capucinus*): Boinski 1993; Boinski and Campbell 1995], and that juvenile and infant monkeys frequently emitted contact calls when they were separated from their mothers (chacma baboons: Rendall et al. 2000; white-faced capuchins: Gros-Louis 2002). Thus, one function of these calls is to prevent separation.

Contact calls represent a major area of interest in the study of vocal communication in Japanese macaques, whereas alarm calls have been the focus of research with respect to other primate species (for review, see Seyfarth and Cheney 1997; Zuberbuhler 2003). In contrast to other primate species in tropical forests or savannas, Japanese macaques are threatened by few potential predators, and thus there were not many studies focusing on the alarm calls of Japanese macaques (but see Masataka 1983).

In early studies of vocalizations, Itani (1963) used his onomatopoetic description to classify six classes and 37 types of calls based on context or function. Green (1975) acoustically analyzed vocalizations using the sound spectrogram and also classified ten classes and 41 subtypes of calls according to their acoustic features. Most vocal communication studies of Japanese macaques have been based on Green's descriptions. Green described contact calls with the greatest detail and referred to a contact call as a "coo call." Coo calls have a tonal acoustical structure, which means that a clear fundamental frequency of their harmonics can be acoustically identified (Figs. 8.1 and 8.2).

Coo calls have been observed in a wide range of contexts among both wild and captive groups, including foraging, grooming, and group movement. Exchanges of

**Fig. 8.1** Juvenile female produces the coo calls

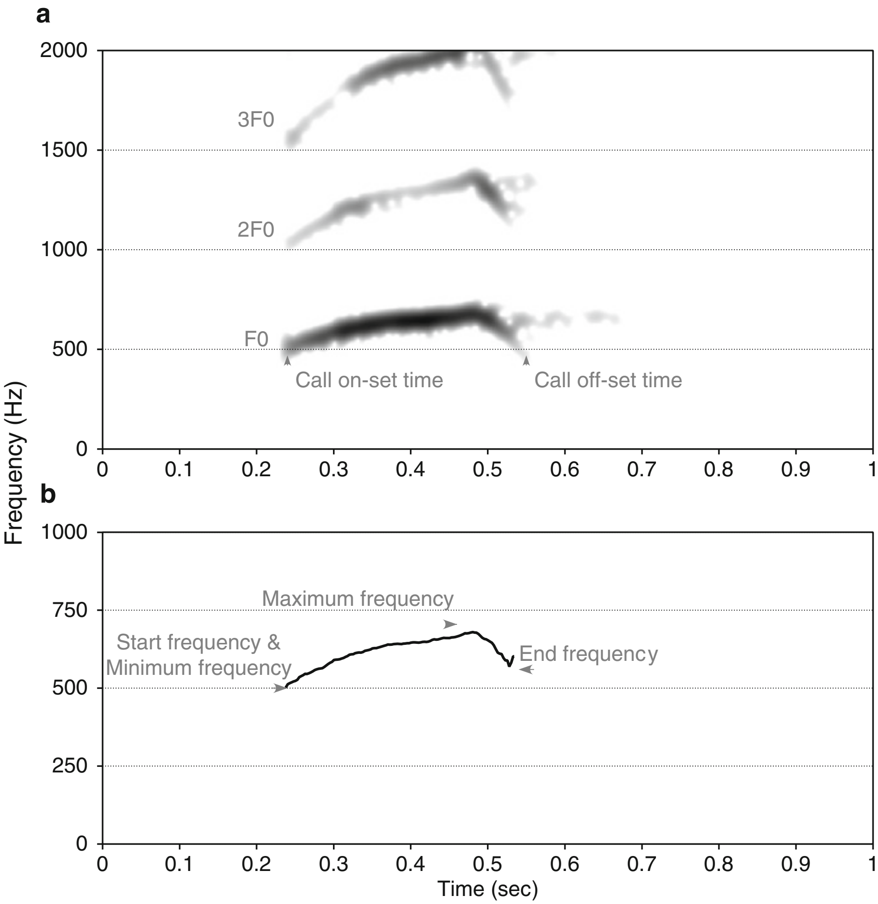

**Fig. 8.2** (**a**) Sound spectrograms of the coo call. In the sound spectrogram, the *x*-axis, *y*-axis, and *color* represent time, frequency, and intensity of sounds, respectively. Coo calls have a tonal/harmonic acoustical structure, which means that a clear fundamental frequency of their harmonics can be acoustically identified. *F0* represents the fundamental frequency of this coo call, and *2F0* and *3F0* are the second and third harmonics of the fundamental frequency, respectively. The fundamental frequency auditory influences the pitch perception of monkeys and humans. The *arrows* show the onset-time and offset-time of coo calls; duration of call is calculated from the difference between the onset- and offset-times of calls. (**b**) Extraction of fundamental frequency. The *curved line* represents the extraction of fundamental frequency of the coo call shown above, which is called the pitch contour. From the pitch contour, we measure various values of fundamental frequency, i.e., start, end, maximum, and minimum frequencies of fundamental frequency. In this figure, the minimum frequency is overlapped with the start frequency

coo calls among group members contribute to avoiding separation from the group and to maintaining group coordination (Mitani 1986; Okayasu 1987). Particularly, Mitani's finding that matriarchs of kin-groups frequently exchanged coo calls with each other clearly supported the vocal functions of maintaining spatial cohesiveness in coo calls. Coo calls exhibit many acoustical variations in various calm contexts. Coo calls have been the most frequently observed communication style practiced by Japanese macaques, irrespective of context.

This chapter reviews recent evidence obtained from studies on vocal communication by Japanese macaques using coo calls, including our fieldwork on vocal communication for 15 years. Previous studies have consistently shown the flexibility and variability of the affiliative vocal communication in wild Japanese macaques. This review discusses the ecological foundations underlying the behavioral variations in the vocal communications of wild Japanese macaques.

## 8.2 Variability in the Vocal Communication of Contact Calls by Wild Japanese Macaques

Studies on vocal communication in Japanese macaques have been conducted in both wild and captive animals from ethological perspectives. Before reviews on coo calls, previous attempts on vocal communications in Japanese macaques are briefly reviewed here.

Previous studies emphasized functions of specific call types and vocal identity discrimination/recognition, similar to other primate species. For a good example of call function studies, Mori (1975) found that specific call types, designated “tonal girney” by Green (1975), are exchanged extensively before grooming interaction. The two macaques frequently exchange the girneys, and then one approaches the others and starts to groom, indicating that girneys are good predictors of their signaler’s subsequent behaviors. Masataka (1989) extended his findings to show that two acoustic types of girneys represented signals of the performer and receiver of grooming. These data indicated that girneys have specific and distinctive motivational referents.

Copulatory vocalizations have been also investigated in the call function studies. Interestingly, it is known that estrous females produce a specific type of vocalizations, which showed modified pitch and longer duration (see Green 1975). Oda and Masataka (1992, 1995) reported that such copulatory vocalizations serve in mate choice by the females.

Some researchers have paid special attention to vocal recognition of macaque identities. Mitani (1986) showed individual differences of acoustic characters in coo calls, and the possibility of the ability of vocal identification by wild macaques. Actually, recent experimental studies of operant conditioning have indicated their ability of vocal discrimination (Ceugniet and Izumi 2004a,b). Maternal ability of recognition of their own infant’s vocalizations has also been confirmed (Masataka 1985; Shizawa et al. 2005).

Each of our field studies on vocal communication relying on coo calls (Sugiura 1993, 1998, 2001, 2007a,b; Koda 2004, 2008; Sugiura et al. 2006; Tanaka et al. 2006; Koda et al. 2008) originated from a different and independent interest—vocal functions, communications rules, vocal development, vocal plasticity, and the origins of human language—rather than a common conceptual framework. However, as we have accumulated various kinds of observational and experimental evidence, we have reached the more general conclusion that macaques adapt their style of communication in the service of maintaining group cohesiveness. In what follows, we review a series of our investigations.

### *8.2.1 Vocal Exchange of Contact Calls as "Conversational" Communication*

Vocal exchange is a characteristic communication style in which a sender produces a vocalization to address a receiver, and the receiver emits a call in response within a brief interval. A fairly strict alternation of calling can occur between two or more individuals, with the participants exhibiting extraordinary precision in their vocalizations. Human conversation, which is organized on the basis of taking turns in the role of speaker, also adheres to this communication style (Goodwin 1981). Many studies of vocal communication have emphasized vocal exchanges in birds (Krebs et al. 1981; McGregor et al. 1992; Beecher et al. 1996), group-living mammals (Janik 2000; Miller et al. 2004), and nonhuman primates (Snowdon and Cleveland 1984; Biben et al. 1986; Masataka and Biben 1987). Vocal exchanges in some nonhuman primates are achieved by taking turns as sender and receiver with precise temporal regularity; thus, the pattern characterizing this type of vocal exchange is somewhat conversational and analogous to that characterizing human conversation.

The first step in our series of studies on Japanese macaques was identifying the temporal rule governing the vocal exchange of coo calls. Sugiura (1993) observed two different populations, the wild groups in the lowland forest of Yakushima Island and the captive group in the Ohirayama semi-open enclosure at Japan Monkey Centre (JMC). The captive group of Ohirayama was introduced from the wild population in lowland forest of Yakushima. He found that macaques in both populations vocally interacted and exchanged calls with other group members using short intercall intervals. He acoustically measured the intervals between two consecutive coo calls produced by two different macaques and by one single macaque. The consecutive coo sequence voiced by the two different macaques was regarded as demonstrating the use of coo calls to initiate and respond to interactions, whereas that voiced by the single macaque was regarded as demonstrating the use of coo calls in repeated attempts to initiate interaction. The interval analysis showed that the same temporal pattern underpinned the exchanges of coo calls between two macaques and the repeated coos voiced by one macaque. When a macaque produced a coo call to address other macaques in the group, the other macaques responded to the initial coo call within approximately 1.5 s (Fig. 8.3). If a macaque did not receive response coo calls from the others, he or she usually repeated coos in intervals of about 2.0 s to elicit responses (Fig. 8.3). Of particular interest is that

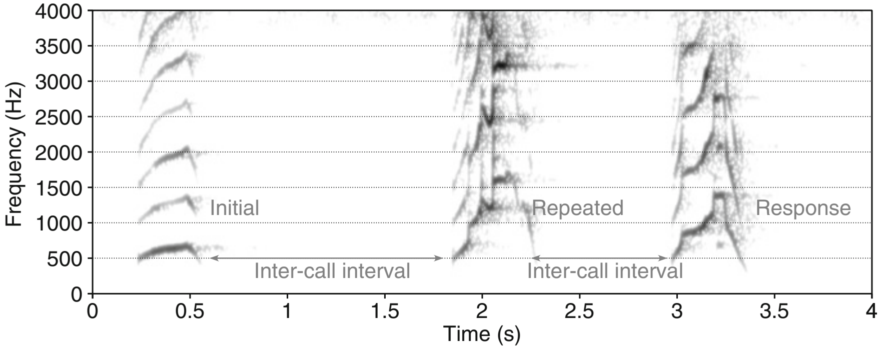

**Fig. 8.3** Sound spectrograms of the sequence of three coo calls. The first (Initial) and second (Repeated) coo calls were emitted by the same caller in an attempt to address another group member. The third coo call (Response) was emitted by the other monkey in response to the second coo call. The second and third coo calls were exchanges between the two monkeys. The *arrows* show the intercall intervals between offset-time and onset-time of the next call. The first intercall interval means the call interval of repeated attempt by the same call, and the repeated call usually occurred approximately within 2.0 s; the second intercall interval means the response time, and the response call occurred within approximately 1.5 s, shorter than the call interval of the repeated attempt. This example illustrates short-term acoustic modification (i.e., the second coo was higher in averaged fundamental frequency and longer in duration than the first coo, whereas the shape of pitch contour and frequency modulation of the second coo were acoustically matched to those of the third coo. (See Koda 2004, 2008; Sugiura 1993, 1998)

the interval between initial and repeated coo calls was longer than 1.5 s, which was the interval between the initial and responsive coo calls. In other words, macaques likely waited for response calls from other members according to temporal rules, and then repeated coo calls after confirming that no response coos had been emitted by group members. These temporal rules of vocal exchange were confirmed in both the Yakushima and Ohirayama groups. This finding indicated that exchanges of coo calls did not occur randomly but were well organized with precise temporal regularity. In the early 1990s, such temporal regularity in animal communication had rarely been reported, with the exception of studies on squirrel monkeys (*Saimiri sciureus*) or pygmy marmosets (*Cebuella pygmaea*) (squirrel monkeys: Biben et al. 1986; Masataka and Biben 1987; pygmy marmosets: Snowdon and Cleveland 1984), but many contemporary studies have confirmed that various species use temporal rules in their vocal interactions. Such temporal regularity has been regarded as a fundamental ability required for communication via vocal exchanges. This study objectively confirmed that macaques' coo calls were produced to address other members and to elicit coo calls in response. Sugiura's early efforts to use temporal analysis to understand the exchange of coo calls underpinned the subsequent approaches to understanding communicative flexibility and variability described in the following sections.

### 8.2.2 Short-Term Acoustic Modifications During Vocal Exchanges

The communication rules underlying coo call exchanges are not restricted to simple temporal regularity. Indeed, further analyses have confirmed the existence of more complex interactions that depend on context. Accumulating evidence about the lowland Yakushima wild groups (Sugiura 1998, 2001; Koda 2004, 2008) has shown that macaques flexibly adapt the acoustic characteristics of pitch or the duration of coo calls according to context, indicating the application of rules for short-term acoustic modifications in coo exchanges.

Sugiura (1993) initially noted that acoustic modification of coo calls occurred during vocal exchanges in addition to the implementation of temporal rules. On the basis of acoustic analysis, he reported acoustic matching, referred to as "vocal mimicry," during the exchange of coo calls. In dyadic exchanges between two adult macaques, responsive coo calls were acoustically similar to the initial coo call in terms of pitch frequency and frequency modulation (frequency differences between the minimum and maximum frequencies; see Fig. 8.3). When macaques initiated interactions with coo calls characterized by a lower and less modulated pitch, the other macaques usually responded with acoustically similar coo calls also characterized by a lower and less modulated pitch; when interaction was initiated with calls characterized by a higher and more modulated pitch, macaques responded with coo calls characterized by a higher and more modulated pitch. Sugiura inferred that macaques were able to immediately adapt to match the preceding coo calls of other macaques in terms of pitch frequency and modulation.

The implication that macaques were able to implement short-term acoustic modifications showed the possibility that monkeys possessed vocal plasticity (i.e., the ability to modify the acoustic features of vocalizations). Vocal plasticity constitutes one of the most remarkable attributes separating the vocal communication of human and nonhuman primates (for review, see Egnor and Hauser 2004). Evidence about the neural structures underlying vocal control has suggested that monkeys cannot voluntarily modify the acoustical structure of their calls independent of their emotional status, indicating the absence of vocal plasticity over a short interval of time (Deacon 1989). In the context of traditional knowledge about vocal plasticity in nonhuman primates, the phenomenon of acoustical character-matching during call exchanges remained controversial.

Sugiura (1998) experimentally replicated the acoustical matching phenomenon preliminarily reported in his early work. He conducted a playback experiment to examine whether monkeys vocally matched the acoustical features of their response calls to those of the calls they heard. In these experiments, six to eight stimulus calls with different fundamental frequency components were played for each of seven females in an attempt to elicit replies from the subjects. Because playback experiments in the 1993 study were difficult to design for each subject monkey, the improved within-subject-designed experiments enabled examination of whether the acoustical properties of fundamental frequency were modulated in exact accordance with the configurations of the initial calls. Results of the acoustic analysis revealed that, given some degree of individual differences, certain properties of the response coo calls were positively correlated with those of the stimulus. More specifically, significant positive results were found for regression analyses involving the frequency modulation of stimuli and that of responses. Thus, the follow-up experiments also confirmed that Japanese macaques matched several of the acoustical features of their replies with those of preceding calls, suggesting that vocal plasticity operated and depended on preceding calls.

Koda (2004) reported on evidence that wild Japanese macaques immediately modified the acoustical features of their contact calls according to a preceding call that failed to elicit a response call from another group member. When a macaque vocalized a coo call but no other members responded, he or she usually repeated the vocalization. Koda analyzed these repeated calling sequences. Acoustic analysis of repeated sequences showed that the repeated call (second call) was higher in fundamental frequency and longer in duration than was the initial call (first call), suggesting the implementation of short-term acoustic modification resembling the acoustic matching phenomenon (see Fig. 8.3).

Short-term acoustic modification plays an important role in functioning, and evidence that macaques most likely immediately modify the acoustic characteristics of coo calls on the basis of preceding contexts is valuable from a neuroanatomical perspective. The acoustic exaggeration manifested in repeated coo calls was more effective in eliciting responses from other members (Koda 2004). Playback experiments involving a single coo call of initial or repeated calls used as playback stimuli produced higher response rates to repeated-call stimuli than to initial-call stimuli. Increased response rates led to more frequent auditory contact, which served to confirm the locations of group members. The function of acoustic matching remains unclear, but similar explanations referencing the enhancement of group contact have been proposed. The ability to locate the origin of coo calls depends on the range of their frequency modulation (Brown et al. 1979). Frequency-modulated vocalizations are appropriate signal forms when the background noise level is relatively high. A frequency-modulated coo call that can be heard by the recipients constitutes a suitable signal for both the original caller and the recipients in terms of transmission through a forest. From a functional perspective, it would be reasonable for recipients to reply to an initial call with acoustically matched calls. Therefore, similar to acoustical exaggeration, acoustical matching would serve to maintain vocal contact among group members. Moreover, the acoustical exaggeration and matching in fundamental frequency do not inhibit their cognitive ability of vocal identity recognition, because the most salient acoustic features are derived from resonance frequency, independent of fundamental frequency (Fitch 1997; Fitch and Fritz 2006; Ghazanfar et al. 2007). Because the vocal identity affects the pattern of coo call exchanging (Mitani 1986), conservation of identical cues in modified signals is important to enhance the vocal exchanging. Short-term acoustical modification should be considered as a kind of behavioral adjustment that strengthens the basic function of contact calls, which involves maintaining spatial cohesion.

The findings of observational and simple experiments were merely descriptions of actual phenomena rather than products of direct investigations of functional or ecological significance. However, the presumed explanations of function have consistently implied a strong internal motivation for maintaining vocal contact among group members. Therefore, the styles of vocal communications likely change, particularly when contact within a group is restricted.

### *8.2.3 Variations Derived from the Detectability of Various Signals*

The distance between sender and recipient constitutes one factor restricting contact between group members because auditory signals experience more attenuation, degradation, and distortion as distance increases (Morton 1975). The interindividual distance likely affects communication styles. In group-living primates, including Japanese macaques, intragroup vocal communication such as coo calls must cover a wide range of distances because group members often remain close together (e.g., while resting) but may also disperse over considerable distances (e.g., while moving or foraging). The acoustic features of vocal signals vary according to the transmission distance to adapt to such environmental constraints (Wiley and Richards 1978; Mitani and Stuht 1998). Recent studies of the lowland Yakushima wild group confirmed that macaques modified the acoustic features of a vocalization according to their distance from other group members (Sugiura 2007b). The proximity of a caller, defined by the distance between the other members and the focal subject macaque, was noted and the vocalizations were recorded. The callers produced coo calls with greater frequency modulations and longer durations when

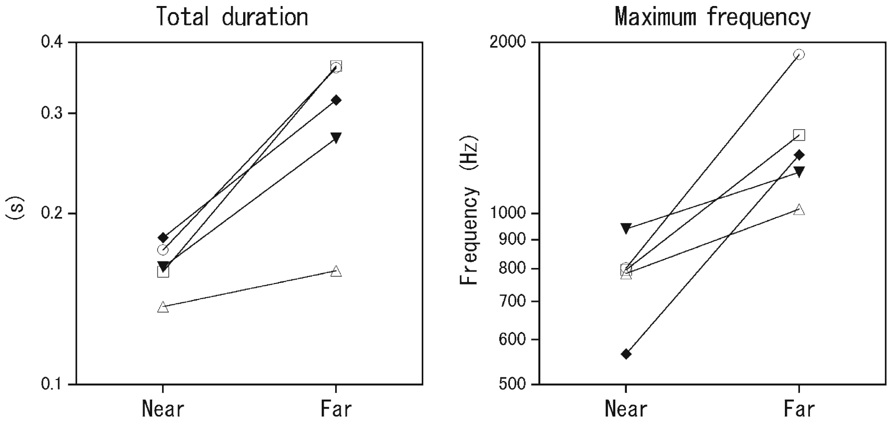

**Fig. 8.4** Means of duration (*left*) and maximum frequency (*right*) of coo calls by each of five individuals when she was near or far from a group member. Each *symbol* represents an individual mean. (Modified from Sugiura 2007b, with permission)

they were far from group members compared to when they were near another member (Fig. 8.4). The results suggested that the calls produced by Japanese macaques varied as a function of proximity to group members, as reflected in the ease with which callers were detected and located.

The interindividual distance also influenced the temporal rules governing exchanges of coo calls (Sugiura 2007a). Following a macaque's spontaneous call, the latency preceding a vocal response by another group member was longer when the subject was farther from group members than when the subject was closer to group members. Furthermore, subjects' repeated calls were separated by longer intervals in the absence of a vocal response, suggesting that subjects were waiting longer for the vocal responses of other group members when response latencies were longer. Thus, the temporal rule for call exchange depended on proximity to other group members.

These two studies suggested the impact of interindividual distances on vocal contacts. Japanese macaques likely adjust their communication styles, including acoustical properties and timing, to aid in effective sound transmission when vocal contacts are obstructed in crucial ways. Japanese macaques are sensitive to the context in which their communications occur.

### *8.2.4 Interpopulation Differences in Vocal Contacts: Environmental Effects*

One of the most widely known examples of environmental influence on vocal communication is interpopulation differences in acoustical structures derived from differences in habitat acoustics. All the aforementioned studies consistently suggested that the wild Japanese macaques in lowland Yakushima were quite sensitive to either vocal or visual difficulties. Such sensitivity was manifested by short-term behavioral adjustments. Given this sensitivity to context, the unique communication styles of this species would have also developed as long-term intraspecies variations in vocal communications if macaques were constantly exposed to either visual or auditory obstructions to their spatial cohesion.

In animal habitats, auditory signals are subject to temporal and spectral degradation, as well as to frequency-dependent attenuation, when sounds travel through the environment (Wiley and Richards 1978). In general, all sources of pattern loss in the frequency domain operate by differentially filtering out certain frequencies during propagation. For example, absorption for a 10-kHz sound in air is approximately ten times greater than is that for a 1-kHz sound. Moreover, in a forest, the amount of propagating sound energy that is lost depends on the size and density of the trees and leaves. The degree of attenuation for frequencies between 1 and 10 kHz is greater in broad-leaved than in coniferous forests (Marten and Marler 1977; Marten et al. 1977).

Noise also alters the spectral composition of a propagated sound by adding new frequency components and masking the sound signals (Marten and Marler 1977; Marten et al. 1977; Waser and Waser 1977; Brenowitz 1982a,b). Wind and insect sounds have been suggested as major sources of noise that usually differ among sites according to spectral composition (Ryan and Brenowitz 1985).

Thus, the characteristics of the habitat environment produce specific patterns of acoustical attenuation, defined as habitat acoustics. For example, birds have clearly been shown to adjust the acoustical characteristics of their songs to suit habitat acoustics (Slabbekoorn and Smith 2002; Slabbekoorn and Peet 2003; Brumm and Todt 2004). Given the ability for vocal leaning in bird species (Catchpole and Slater 2008), the adjustment of acoustical properties to habitat characteristics constitutes a reasonable way to ensure the efficiency of vocal communication.

The influence of habitat acoustics on vocalization has been also reported in several nonhuman primates species [blue monkeys (*Cercopithecus mitis*): Waser and Brown 1984, 1986; gray-cheeked mangabeys (*Cercocebus albigena*), savanna monkeys (*Cercopithecus aethiops*), and yellow baboons (*Papio cynocephalus*): Brown et al. 1995; pigmy marmosets: de la Torre and Snowdon 2002, 2009; chimpanzees (*Pan troglodytes*): Mitani et al. 1992, 1999; orangutans (*Pongo* spp.): Delgado 2007]. These findings have been explained in terms of the same mechanisms by which habitat acoustics shape the acoustic characteristics of birds.

One of the direct ways of testing environmental effects on contact calls is to compare vocal communications among populations inhabiting different environments. Japanese macaques are a suitable species for testing the influence of environment on vocal behavior because members of this species are distributed from warm-temperate to cool-temperate zones of Japan in forests that vary from seashore to alpine locations (Yamagiwa 2008; see also Chaps. 5 and 7). In addition, many captive groups are kept in zoos and are available for comparison with the wild original groups. Therefore, it is possible to choose among populations inhabiting a wide variety of environments, ranging from open-space enclosures to tree-crowded forests.

Because the function of contact calls is strongly related to the spatial cohesiveness of the group, habitat environments shape the development of different styles of vocal communication via contact calls. On the basis of this assumption, we conducted three investigations of the behavioral adjustments made to vocal communications in different habitat environments (Sugiura et al. 2006; Tanaka et al. 2006; Koda et al. 2008). The physical structure of the forest or artificial habitat potentially influences vocal communication relying on contact calls. Our three investigations found adjustments in response to habitat environments in terms of both acoustical quality and quantity.

Comparisons of captive and wild populations showed that Japanese macaques likely changed acoustical features of their communications according to the acoustics of their habitat (Sugiura et al. 2006; Tanaka et al. 2006). The first purpose of our studies of interpopulation differences was to examine the possibility that the acoustical properties of the contact call were acquired through a kind of learning process. To avoid factors of genetic transmission, we compared acoustical features of the coo calls emitted by two populations: the wild group of lowland Yakushima and the captive group of Ohirayama at JMC.

The Ohirayama group originated from the wild population of lowland Yakushima but has been separate for more than 34 years. Cross-sectional investigations of females

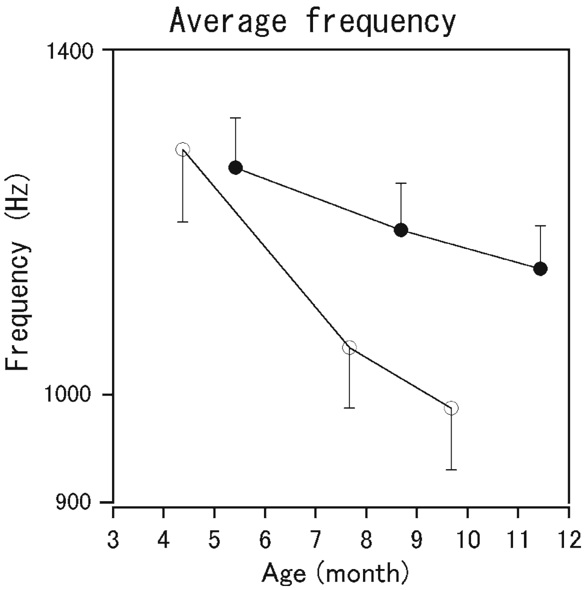

**Fig. 8.5** Mean and SD of average frequency of coo calls during development in Ohirayama group (*closed circles*) and Yakushima group (*open circles*). The means and SDs are calculated from individual averages of six individuals in each group at three developmental age categories. (Modified from Tanaka et al. 2006, with permission)

ranging from 0 to 18 years of age have consistently reported lower pitch frequency among individuals of all ages in the Ohirayama group than among those in the Yakushima group. Subsequent developmental analyses of longitudinal comparisons revealed that intergroup differences in coo calls were not observable at 3–4 months after birth but were already developed by approximately 6–7 months after birth (Fig. 8.5).

Because a previous study reported that acoustic features are correlated with body weight or age (Inoue 1988), their differences seem to be explained simply by the body weight differences among these groups. However, lack of correlation between body weight and frequency was reported in young immature female Japanese macaques (Masataka 1994), implying the possibility that immature macaques flexibly change the acoustic structures of the coo call. Given that the rate of body weight range increase is generally constant from birth to the fourth year (Inoue 1988; Kurita et al. 2002), these findings suggested that the population-specific acoustic features of coo calls were likely formed after birth through the influence of social or environmental factors.

Subsequent research on habitat acoustics has supported explanations of interpopulation differences between Yakushima and Ohirayama that rest on differences in habitat environments (Sugiura et al. 2006). Habitat acoustics were measured in terms of the degree to which pure tones (250–8,000 Hz) were transmitted, and the coo calls of the population in each habitat were measured using a sound level meter. Pure tone sounds with lower frequencies were transmitted more efficiently in the Ohirayama enclosure than in the Yakushima lowland forests. Consistent with this finding, low-pitched coo calls showed significantly better transmission than did high-pitched calls in the Ohirayama enclosure. On the other hand, these differences did not emerge in the Yakushima lowland habitat. The low-pitched coos of Ohirayama must have been suitable for effective transmission within this habitat.

These two studies indicated that the low-pitched coo calls in Ohirayama established in response to the enclosure's acoustics, in which low-frequency sounds were better for transmission. This is the first evidence showing that Japanese macaques adjust the acoustic features of coo calls according to habitat acoustics, and also surprisingly indicated the possibility of vocal learning in wild Japanese macaques. As vocal learning ability has been a controversial matter in Japanese macaques (for positive evidence, see Masataka and Fujita 1989; for negative evidence, see Owren et al. 1992, 1993), these findings provided some positive evidence of vocal learning in nonhuman primates.

The correlation between acoustical structures and habitat acoustics provides a clear example of the influence of habitat environment on vocal communication. An additional potential correlation concerned the function of contact calls (i.e., the correlation of call rates and habitat visibility). Monkeys were likely to simply increase their call rates when visual or auditory access to contacts was extremely restricted, using vocalization to ensure the cohesiveness of the group. One early examination of the rate of coo calls implied a higher rate of coo calling in the Yakushima population than in the captive population (Okayasu 1987), suggesting that the dense vegetation of the lowland forest of Yakushima restricted visual contact and enhanced the rate with which contact calls were uttered. In other words, call rates probably increased to ensure spatial cohesiveness because individuals often became separated from the group in habitats with restricted visibility. However, few studies have investigated the influence of habitat visibility, whereas many have investigated the effects of a forest habitat on the acoustical features of contact calls (for review, see Ey et al. 2009).

In a recent study, we approached interpopulation differences from a quantitative perspective, focusing on the relationship between call rates and habitat visibility (Koda et al. 2008). To examine the influence of habitat visibility on coo call rates, both factors were measured for the wild groups of lowland evergreen forest in Yakushima and a group in the deciduous forest in Kinkazan Island. The environmental evaluation showed that visibility was significantly more restricted in Yakushima than in Kinkazan. Our observations of coo call rates generally indicated higher call rates in Yakushima than in Kinkazan, corresponding with the findings on habitat visibility (Fig. 8.6).

Interestingly, call rates for different activities differed between the two areas. Interpopulation differences were more pronounced during feeding and moving than during grooming. Moreover, differences in call rates were found only in adult macaques and not in juveniles. These interactions between activity and age support the importance of habitat visibility for contact calls. Because individuals within a group usually disperse during foraging or moving and show spatial cohesiveness

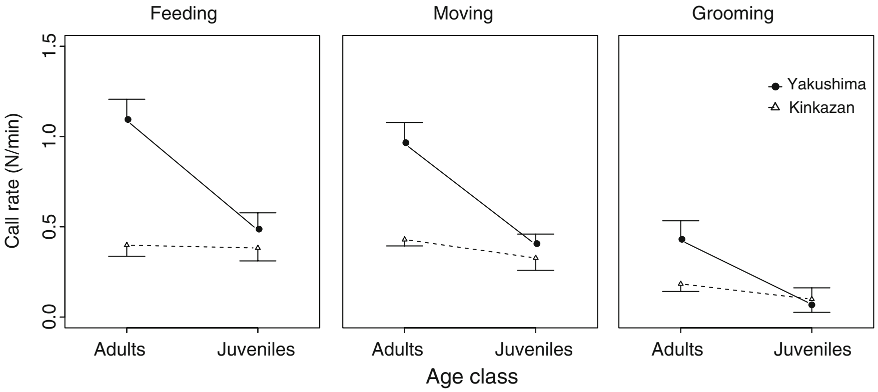

**Fig. 8.6** Coo call rates of female Japanese macaques for feeding, moving, and grooming activities. Mean values with standard errors represent averaged values among the subject's mean call rate. *Closed circles* represent the wild groups in the lowland forest of Yakushima; *open triangles* represent the Kinkazan population. (Modified from Koda et al. 2008, with permission)

during grooming, the degree to which habitat visibility is influential likely differs among these activities. The difference between adults and juveniles is reasonable because adult females normally have contact with other adult females in the group, whereas juveniles normally remain in close proximity to their mothers (Nakamichi 1989, 1996). Therefore, this study suggested that habitat visibility acts as a primary determinant of coo call rates, interacting with such behavioral and contextual factors as activity and age.

The three studies implied that environmental characteristics such as habitat acoustics and visibility actively generated interpopulation differences in both acoustical features and call rates. The Japanese macaque likely adapts its communication styles to fit environmental conditions to maintain spatial cohesion.

## 8.3 What Is the Principal Factor Generating the Behavioral Variations in Communications with Coo Calls?

### *8.3.1 Vocal Adjustments of Long-Term and Short-Term Scales*

Our findings about Japanese macaques demonstrated that communication via coo calls was subject to a wide variety of behavioral adjustments. All behavioral adjustments in coo calls were achieved on the basis of the macaque's ability to modify these calls; however, different mechanisms should underpin the different adjustments in vocal behaviors. Recent reviews of the adaptation of vocal behavior to environment have proposed that vocal modifiability is classified into two dimensions according to the time scale involved: short-term and long-term vocal plasticity

(Brumm and Slabbekoorn 2005). For example, by these classifications, interpopulation differences in vocalizations should arise from long-term causes, whereas acoustical matching occurring during the vocal exchanges between two macaques should be treated as short-term phenomena. This idea is not unique, but rather resembles the traditional framework of ethology known as "Tinbergen's four questions" (Tinbergen 1963). Long-term vocal adjustment pertains to developmental changes through the learning process (i.e., vocal learning), whereas short-term adjustment pertains to proximate causation (i.e., the psychological or physiological mechanisms underpinning vocal control). The behavioral responses involved in vocal communication were also classified into two categories, modification of acoustic features and increase/decrease in call rates. Thus, different causal factors act in combination on contact calls, inducing both short- and long-term vocal variability.

### *8.3.2 "Separation Risks" and "Motivation to Coordinate the Group"*

In both the short and the long term, Japanese macaques modify/adjust their vocal behavior so that such behavior manifests in appropriate forms (acoustic modifications and changes in call rates). Given that the basic function of calls involves the maintenance of cohesiveness, all behavioral adjustments can be thought to serve as increasing the efficiency of vocal contacts. The variability or flexibility characterizing their communication styles suggests that Japanese macaques are quite sensitive to spatial separation. We propose a fundamental external cause, "separation risks," as well as an internal cause, "motivation to coordinate the group," and tentatively hypothesize that the interaction between these causes constitutes the principal factor underlying the variability in contact calls. Thus, contact calls would be strongly affected by increases in either the risk of separation or the need for group coordination.

Separation risks are defined as the probability of a visual or auditory separation between a macaque and her or his own group. For example, the degree of visual separation constitutes one of the simplest representations of separation risk. Some of our findings are actually explained by the degree of visual separation. Dispersion among group members, characterized by relatively large interindividual distances (Sugiura 2007a,b), restricts the visual contact among macaques, increasing the separation risks. Poor visibility on lowland evergreen forest in Yakushima suggested that this environment was characterized by potentially greater separation risks than was Kinkazan (Koda et al. 2008).

Previous studies on several primate species reported that visual separation during group traveling led to an increase in call rates and a modification in the acoustic characteristics of contact calls. The rate of contact calls increased as distance among group members increased in several species (Snowdon and Hodun 1981; Boinski 1991, 1993; Boinski and Mitchell 1992; Boinski and Campbell 1995; Cheney et al. 1996; Rendall et al. 2000). Distance effects on the acoustical features of contact calls have also been confirmed in many species of nonhuman primates in both naturalistic and experimental settings. Increasing the distance between caller and recipient(s) led to more pronounced, longer-lasting, and/or higher-pitched calls [squirrel monkeys: Masataka and Symmes 1986; ring-tailed lemers (*Lemur catta*): Oda 1996; pygmy marmosets: Snowdon and Hodun 1981; common marmosets (*Callithrix j. jacchus*): Schrader and Todt 1993]. These findings, along with our results on wild Japanese macaques (Sugiura 2007b; Koda et al. 2008), suggested that auditory contact effectively maintained spatial cohesion, especially under conditions of low visibility.

Context-dependent vocal adjustments are also fundamentally explained by short-term change of degrees of separation risks. Our studies (Sugiura 1998; Koda 2004) indicated context-dependent vocal adjustments in short-term scales, that is, acoustic modification with response to preceding context before call emission. Given the correlation between pitch and interindividual distance, the preceding context where macaques hear the higher-pitched and frequency-modulated call likely suggests the context where interindividual distances broaden. Similarly, the context in which macaques failed to elicit others' reply calls probably indicates that the caller macaque was exposed to a higher risk of separation. Consequently, preceding behaviors of the other member indirectly represent the degree of separation risks in short-term scales. The evidence that monkeys could modify the acoustic structures of calls depending on the various contexts has not been sufficiently reported in nonhuman primates. However, some reports on wild chimpanzees suggested context-dependent vocal modification during their long-distance call exchanging (Mitani and Brandt 1994; Notman and Rendall 2005). Recently, experimental studies have indicated that the context where the monkeys are exposed to environmental noise or acoustic interference directly affects the acoustic structure of calls [common marmoset: Brumm et al. 2004; cotton-top tamarin (*Saguinus oedipus*): Egnor and Hauser 2006; Egnor et al. 2006, 2007]. Given the accumulating evidence of context-dependent vocal adjustments, the acoustic variety confirmed in the wild situation is likely induced by the variation of separation risks.

Separation risks are not sufficient for explaining all phenomena of vocal dynamics of contact calls. Although separation risks reflect the external conditions of monkeys, including the degree of visual separation, these risks differentially influence the vocal communication of each individual according to age, sex, social status, and other social factors.

From the developmental aspects, adult females emit and exchange the contact call more frequently than juvenile and infant females (Koda et al. 2008). The previous empirical evidence shows the developmental change or age-class differences on the contact call communication at least for female Japanese macaques, suggesting that the degree of separation risk likely depends on the age class. The early work on contact calls performed at Yakushima confirmed that adult males emitted far fewer calls than did adult females (Mitani 1986). Because the separation risks for males and females in the same group are governed by similar conditions, these data indicated that male macaques were less sensitive to separation risks and the need to maintain spatial cohesion than were female macaques, suggesting that males were less motivated to coordinate the group than were females. Thus, evaluation of separation risk differs among individuals.

Boinski and Garber (2000) proposed a similar notion, that vocal communication by contact calls was determined primarily by the "motivation to coordinate group travel." They suggested that increased motivation to coordinate group travel led to higher call rates, louder calls, longer travel signals, greater fluctuation and modulation in acoustical signals, and more exaggerated movements and monitoring of recipient responses. Motivation to coordinate group travel might be understood as an internal state or as an emotional mechanism underlying the maintenance of group cohesiveness.

Thus far, however, the existence of such motivation has not been confirmed. Evidence of the correlation between emotional status and acoustical characters (Fichtel et al. 2001) might support the role of motivation to coordinate the group. An increase in emotional aversion was paralleled by an increase in pitch frequency. The detectable, longer-lasting, and/or higher-pitched calls reported by several studies (Snowdon and Hodun 1981; Masataka and Biben 1987; Schrader and Todt 1993; Oda 1996; Sugiura 1998, 2007b; Koda 2004) might have resulted from the motivational changes that accompanied separation risks in the context of aversive states.

In summary, we propose that two fundamental causes underpin these phenomena: the risk for separation and the internal motivation to coordinate the group. Macaques are always internally motivated to evaluate separation risks. The degree of separation risk is determined primarily by environmental conditions or behavioral contexts in both the long and short term. However, separation risks are differentially evaluated because internal motivation depends on age, sex, and other social factors. Separation risks and internal motivation induce variations in vocal communications relying on contact calls and likely determine the type of vocal communication used in wild primate social groups (Fig. 8.7).

## 8.4 Further Directions

Our studies have found that macaques make a wide variety of vocal adjustments to coo calls on both a short- and long-term basis; these include modifications of acoustic characters and increases in call rates. Our confirmatory evidence was restricted to female subjects because of clear sex differences in contact call communication. Indeed, adult male macaques rarely vocalized via coo calls in wild groups (Mitani 1986). In other words, sex differences and other social factors have proven to be insufficient for understanding Japanese macaques. Social influences and life histories in a matrilineal society should be considered in future research on vocal communication.

Indeed, social framework influences intragroup vocal communications (Snowdon and Hausberger 1997), and sex differences likely determine the pattern of vocal communication. Adult male primates, including Japanese macaques, usually produce fewer contact calls than do adult females (Boinski and Garber 2000). Such sex differ-

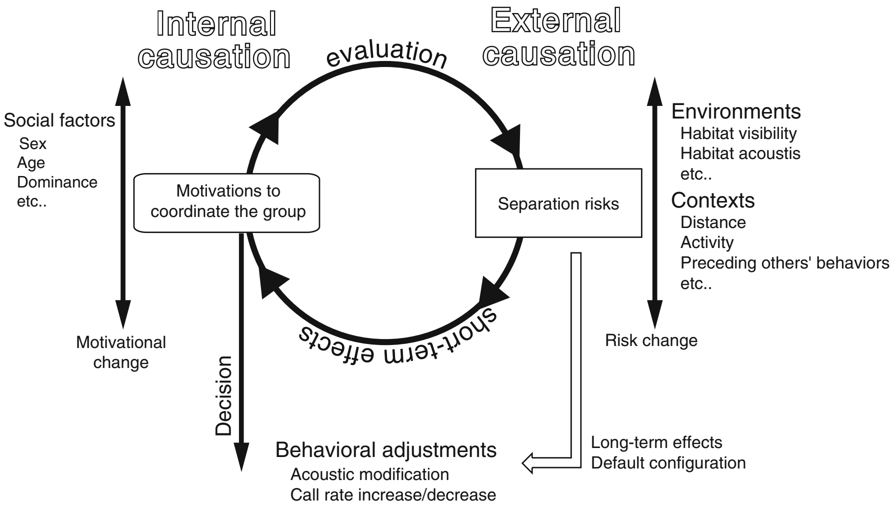

**Fig. 8.7** The two fundamental causes of variation in vocal communications: separation risks and motivation to coordinate the group. On the internal side (*left side*), monkeys always evaluate the separation risks (*right side*). The internal motivation likely changes according to age, sex, and social factors. The degree of separation risk is determined primarily by environmental conditions or behavioral contexts in both long- and short-term time scales. The combination of separation risks and internal motivation induces the variation in vocal communications by contact calls and likely determines the type of vocal communication used by wild primate social groups

ences in contact calls are no doubt caused by sex differences in social status or roles vis-à-vis group cohesiveness. In general, robust sex differences have been reported in the degree of active coordination of group movements. Wrangham (1980) argued that females are important in deciding the direction and timing of movements in female-bonded species. Females appear to be determinant in coordinating group movements in many primate species (Erhart and Overdorff 1999). These data are likely related to the fact that females are often the philopatric sex, whereas males are the immigrating sex (Leca et al. 2003). Consequently, coordination of group movements should differ in adult females and males. In the matrilineal societies of Japanese macaques, the social status of males dramatically changes upon emigration from the natal groups, strongly suggesting a dramatic change in the motivation to coordinate the group. We hypothesize that the call rates of male macaques dramatically decrease during emigration periods; however, developmental changes in the production of coo calls remains an open question. Future research should attempt to analyze the developmental course of sex differences in the production or rates of coo calls in terms of correspondence with the life histories of macaques.

Intergroup comparisons should examine social influences on coo calls. Because our data on interpopulation differences were obtained in different locations and environments, they are insufficient for distinguishing the influence of social factors from that of environmental factors. Fortunately, the population of the lowland evergreen forest in Yakushima is ideal for testing intergroup differences in influences on vocal behavior because various groups with varying group sizes and individual composition have been longitudinally observed (Yamagiwa 2008). For example, comparisons among groups of different sizes or compositions can be made to examine the effect of group size on vocal behavior. Because the primary function of coo calls is to enhance the coordination of group movements, the call rate is likely influenced by the number of potential partners within a group. Small compact groups are more spatially cohesive than are large dispersed groups, and thus direct visual contact with most members should be possible in the former, leading to decreased call rates. If, however, a macaque in a small group loses sight of the other members, she or he likely produces highly emotional calls that are acoustically highly modulated. Thus, we predict that macaques in small groups show greater sensitivity to losing their groups owing to lower separation risks. On the other hand, separation risks are likely higher in large dispersed groups, leading to higher call rates. These predictions should be tested to compare the effect of size or composition.

Comparisons according to variations in group coordination or group movement are no doubt essential for understanding the ecological foundations of contact call communication. Reviews of primate group movement (Boinski 2000) have summarized the sources of variation in group travel movements. Boinski (2000) noted seven sources of variations in the patterns of group movements. These sources include psychological factors (individual preference, susceptibility to predation), social factors (age, sex, dominance, group composition, and group size), and environmental factors (habitat quality and structure, predation). Variations in contact calls must result from responses to changes in the conditions affecting group cohesiveness or movement.

In this chapter, we focused on the affiliative vocal communication, that is, contact calls; however, other types of calls are essential for their social life. Given that the strategies for antipredation or mating success are fundamental for animal survival, vocal communications by alarm or copulation calls have been the central issues in other primates, mammals, and birds (Bradbury and Vehrencamp 1998). Japanese macaques are no exception. Although vocal communication by contact calls have been dominantly investigated, studies on the other types of vocal communications have been insufficient yet in this species from the comparative perspectives of evolution of communication signals. In addition to contact calls, considerations of the other types of communication are no doubt necessary to understand the signal design of Japanese macaques.

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# Chapter 9: Cultured Japanese Macaques: A Multidisciplinary Approach to Stone Handling Behavior and Its Implications for the Evolution of Behavioral Tradition in Nonhuman Primates

**Michael A. Huffman, Jean-Baptiste Leca, and Charmalie A.D. Nahallage**

## 9.1 Introduction

The concept of culture (also referred to as behavioral tradition) in animals was first proposed in 1952 by the founder of primatology in Japan, Kinji Imanishi, who predicted that culture should be present in all socially living animals. By the early 1950s, provisioning and individual identification of all members of several Japanese macaque (*Macaca fuscata*) groups across Japan were accomplished, including those of Koshima, Takasakiyama, Arashiyama, and Minoo. The practice of long-term comparative and collaborative research was begun, one of the many early contributions by Japanese scientists to the field of primatology (Huffman 1991; Yamagiwa and Hill 1998; Takahata et al. 1999; see also Chap. 1). Provisioning provided the first outdoor laboratory situation for recording the process of behavioral innovation and diffusion of behaviors in a novel environment, and research at these sites has contributed much to our understanding of the patterns of diffusion of innovative behavior in primates (for reviews, see Itani and Nishimura 1973; Nishida 1987; Thierry 1994; Huffman and Hirata 2003).

Perhaps two of these most widely cited examples of evidence for culture in Japanese macaques, and arguably all animals, is the innovation and transmission of sweet potato washing and wheat washing behavior in the Japanese macaques on Koshima Islet, Miyazaki Prefecture, Kyushu (Kawai 1965). By September 1953 on Koshima, almost 2 years after provisioning began, the macaques were regularly

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eating the sweet potatoes and wheat passed out to them on the beach. At this time a young female, *Imo*, was observed to begin to carrying soiled sweet potatoes to a small stream and to wash off sand and dirt before eating (Kawai 1965). This combination of provisioned novel foods and access to water by all individuals set the stage for the transmission of food washing behavior. The first individual other than *Imo* to display this behavior was a playmate, followed by *Imo*'s mother and other playmates, eventually spreading widely to others of the group. Next, *Imo* began to wash potatoes in sea brine instead of freshwater, supposedly to season them (Kawai 1965). The next behavior innovation to be recorded on Koshima was wheat washing behavior. Again, it was *Imo* who was first observed to exhibit this habit, whereby sand grains and wheat were separated from each other by dropping handfuls of these mixed ingredients into puddles of water on the beach or directly into the ocean. The behavior spread within the group along similar lines as potato washing.

Again on Koshima, the habit of fish eating was observed from its innovation and followed as it spread throughout the group (Watanabe 1989). A clear difference in the initial route of transmission was noted between fish eating and potato or wheat washing behaviors. That is, fish eating first appeared in an adult male living in the group's social periphery. The behavior spread to an old female, and from her the habit is reported to have eventually diffused to members within the group's social center (Watanabe 1989).

More recent work in Japanese macaques has focused specifically on the innovation and diffusion of new group-specific behavioral traditions in free-ranging provisioned groups (Huffman 1984, 1996; Huffman and Quiatt 1986; Tanaka 1995; 1998; Leca et al. 2007a). For example, Tanaka (1995, 1998) studied the changes at the individual and group levels in louse egg-handling techniques (e.g., "combing" and "pinching") to facilitate their removal during grooming in a free-ranging group of Japanese macaques living at Jigokudani Monkey Park, Shiga Heights, Nagano Prefecture. On the one hand, louse egg-handling skills were not fixed for each individual, but they changed over time. The successive shifts in the adoption of different techniques by the same individual may not only reflect structural and functional aspects of the behavior, but also some form of individual learning (Tanaka 1998). On the other hand, the maternally skewed distribution of different louse egg-handling variants strongly suggests the social transmission of behavior, possibly via imitative learning (Tanaka 1995). For example, one female's new technique was later adopted by her sister, daughters, and granddaughter. Because Japanese macaques show a high degree of kin bias and/or favoritism in most behaviors and interactions, compared to other macaque species (Chapais et al. 1997), it is not surprising that many innovative behaviors were shown to first diffuse widely within kin lineages before being adopted by unrelated individuals (Watanabe 1989; Kawai et al. 1992; Tanaka 1995).

Dental flossing has been reported in a group of long-tailed macaques (*Macaca fascicularis*) in Thailand (Watanabe et al. 2007). The use of hair as dental floss to remove food remains stuck between the teeth, dental flossing is a form of tool-use (sensu Beck 1980) and may be considered a form of self-medication *(*sensu Huffman 2007). It has been discussed as a group-specific behavior in terms of culture, and social learning has been invoked by clear descriptions of mothers exaggerating their flossing actions in the presence of their offspring, supposedly to facilitate the learning of the behavior by infants (Watanabe et al. 2007; Masataka et al. 2009). Recently, Leca et al. (2010a) reported the first case of dental flossing behavior in a Japanese macaque at Arashiyama, Kyoto. Although this behavior was performed frequently by a central middle-ranking middle-aged female during her grooming interactions, and appeared several years ago, it remains idiosyncratic to its innovator, and up to now has not spread to other group members.

Extensive collaborative field studies of socially learned behaviors among the great apes have also documented complex behavioral traditions in chimpanzees (Tomasello 1990; Whiten et al. 1999) and orangutans (van Schaik et al. 2003a).

Evidence for socially mediated learning and culture in many species now exists, including the great apes, New World monkeys, rats, cetaceans, birds, and fish (see Fragaszy and Perry 2003). These examples range from the opening of milk bottle caps by British tit birds (Fisher and Hinde 1950, 1952) and pinecone stripping by Israeli black rats (Aisner and Terkel 1992; Terkel 1996) to examples including transmission of behaviors sometimes leading to social traditions as diverse as mate choice in guppies (Dugatkin 1996), new vocalizations in ravens (Enggist-Dueblin and Pfister 2002), feeding techniques of Tonkean macaques (*Macaca tonkeana*; Drapier and Thierry 2002), abnormal behaviors of captive rhesus macaques (*Macaca mulatta*; Hook et al. 2002), and prey capture by killer whales (Rendell and Whitehead 2001). All these studies have investigated determinants of cultural behavior, including innovation, transmission, acquisition, developmental constraints thereof, long-term maintenance, and intergroup variation. However, none has considered the role of all these factors in an integrated framework of social learning.

There are two basic approaches to the study of social learning, the underpinnings of culture. The first focuses on underlying mechanisms, that is, “how” the information is transferred between two individuals. Under a controlled experimental setting, a naïve subject, faced with a problem-solving task, is given the opportunity to observe an experienced subject and learn from its behavioral strategies (Custance et al. 1999). The second approach focuses on the pathway of behavioral diffusion under natural conditions in a stable social group, that is, from “whom” the information is transferred (Biro et al. 2003). Interindividual tolerance allowing spatial proximity, frequency of the behavior performed, and the attention paid to the behavior are essential factors to predict the speed of diffusion of a novel behavior and the pathway of transmission (Coussi-Korbel and Fragaszy 1995; Huffman and Hirata 2003; van Schaik et al. 2003a). However, not only social, but also environmental, demographic, and developmental, constraints can affect the efficiency and speed of acquisition and diffusion of a particular behavior (Huffman and Hirata 2003). Thus far, only the study of stone handling (SH) behavior in Japanese macaques has embraced all these determinants into the understanding of a single cultural behavior. Our long-term study supports the idea of SH culture and provides insights into the nature of social learning, its role in the spread of behavioral innovations, the factors influencing intergroup behavioral variation, the emergence and transformation of culture, and the potential importance of culture in the process of biological evolution.

## 9.2 Stone Handling Behavior

SH is a seemingly nonadaptive solitary object play activity (Huffman 1984, 1996; but see Nahallage and Huffman 2007a and Sect. 9.5.8). SH consists of manipulation of stones in various ways, including rubbing or clacking them together, pounding them onto other hard surfaces, picking them up and rolling them together in the hands, and cuddling, carrying, pushing, or throwing them (Fig. 9.1 and Table 9.1). Currently, 45 different behavioral patterns are documented in Japanese macaques (Leca et al. 2007a).

SH is reported to occur in four captive groups and six provisioned free-ranging groups across Japan, and still other sites are known but have not yet been systematically investigated. This behavior has been followed for 30 years across multiple generations in the Arashiyama group, Kyoto, Japan, beginning from its innovation (Huffman 1984, 1996; Leca et al. 2007a). In contrast to potato washing, SH was first transmitted horizontally among playmates. Transmission began to occur vertically from elder to younger individuals around 1984. Since then, SH has been acquired by every infant in the group, but never by individuals over 5 years of age.

## 9.3 Long-Term Observation of the Arashiyama Group

### *9.3.1 Innovation*

Japanese macaques have been studied at Arashiyama since 1954, after macaques were enticed to narrow down their wide seasonal ranging patterns when provisioning was successfully initiated at the Iwatayama Monkey Park (Huffman 1991). In spite of the intense history of research at the site by many scientists in succession, SH was not noted until December 7, 1979 (Huffman 1984). The first individual recognized to perform this behavior was the 3-year-old, middle-ranking female *Glance-6476* (Fig. 9.2). She had brought several flat stones from the forest and was gathering them together and scattering them about with the palms of her hands on the open ground of the provisioning site. This was the first and the last time that SH was observed by Huffman during a 12-month study lasting up to September 1980.

### *9.3.2 Transmission*

In October 1983, when Huffman returned again to Arashiyama to resume research, SH had already diffused to many members of the group and had become a daily

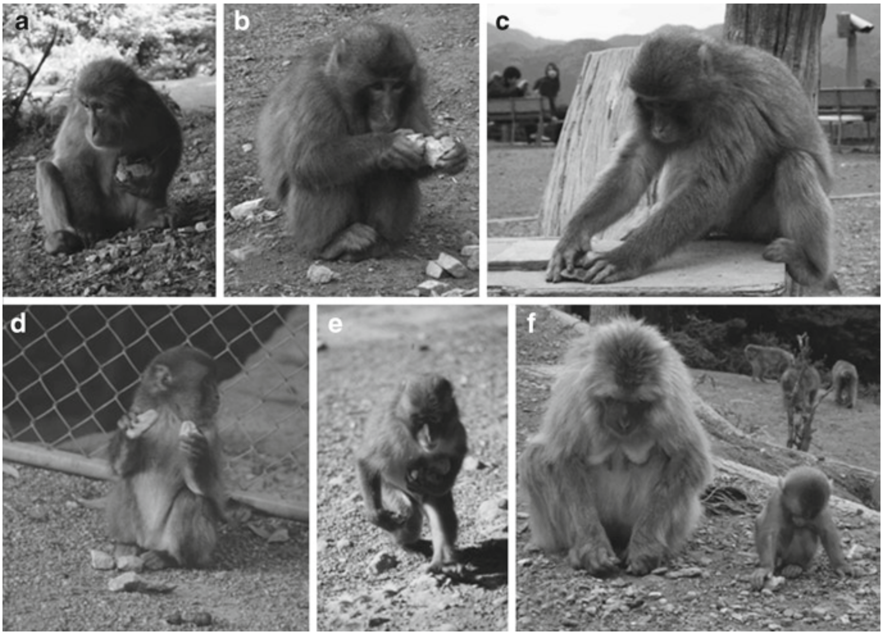

**Fig. 9.1** Five stone handling (SH) patterns (**a**, cuddle; **b**, rub together; **c**, rub on surface; **d,** clack; **e**, carry;) and a mother–infant dyad performing SH simultaneously (**f**). (Photographs **a, c** and **f**, courtesy of J.-B. Leca; photographs **d** and **e**, courtesy of M.A. Huffman; photograph **b**, courtesy of N. Gunst)

occurrence. SH was classified into eight basic behavioral patterns: gathering, pick up, scatter, roll in hands, rubbing stones, clacking, carry, and cuddle (Huffman 1984). By 1985, an additional nine behavioral patterns were also recognized, with six of those patterns being variations of the original eight (pick up and drop, rub of surface, flinting, pick up small stones, rub with hands, and grasp with hands). The three new behaviors were toss walk, move and push, and grasp walk, all behaviors considered to reflect an increasing familiarity with stones in general as the practice of SH spread and became a substantial part of the individual and the group daily activity.

In June 1984, 49% (115/236) of the group exhibited SH and by June 1985, 60% (142/236) of the group members born before June 1984 were verified to be new SH users. Eighty percent (92/115) of the individuals observed were born between 1980 and 1983, after the first record of SH was made in 1979. The remaining 20% were young adult males ($n = 6$, 4.5–8.5 years old), young adult females ($n = 6$, 4 years old), and adult females ($n = 11$, 5+ years old).

The evidence strongly suggests that SH originated from the *Glance* kin-group, given that other than *Glance-6476*, the first female observed to exhibit SH in 1979, the only older individuals noted to perform SH were her two female cousins, *Glance-6775* and *Glance-6774*, and a lower-ranking female, *Blanche-596475*. In contrast to potato washing and wheat washing behavior, two of the earliest examples of cultural traditions in Japanese macaques, no individuals have ever been noted to acquire SH behavior after they reached the age of 5 years. This finding supports our

**Table 9.1** Forty-five stone handling (SH) patterns performed by Japanese macaques and categorized according to general activity patterns

| Category | Name | Definition |
|---|---|---|
| Investigative activities | Bite | Bite a stone |
| | Hold | Pick up a stone in one's hand and hold on to it, away from the body |
| | Lick | Lick a stone |
| | Move inside mouth | Make a stone move inside one's mouth with tongue or hands |
| | Pick | Pick up a stone |
| | Put in mouth | Put a stone in one's mouth and keep it some time |
| | Sniff | Sniff a stone |
| Locomotion activities | Carry | Carry a stone cuddled in hand from one place to another |
| | Carry in mouth | Carry a stone in mouth while locomoting |
| | Grasp walk | Walk with one or more stones in the palm of one or both hands |
| | Move and push/pull | Push/pull a stone with one or both hands while walking forward/backward |
| | Toss walk | Toss a stone ahead (repeatedly) and pick it up while walking |
| Collection or gathering activities | Cuddle | Take hold of, grab or cradle a stone against the chest |
| | Gather | Gather stones into a pile in front of oneself |
| | Grasp with hands | Clutch a stone or a pile of stones gathered and placed in front of oneself |
| | Pick up | Pick up a stone and place it into one's hand |
| | Pick and drop | Pick up a stone and drop it repeatedly |
| | Pick up small stones | Pick up small stones and hold them between fingertips (like the picking up of wheat grains) |
| Percussive or rubbing sound-producing activities | Clack | Clack stones together (both hands moving in a clapping gesture) |
| | Combine with object | Combine (rub or strike) a stone with an object different from a stone (food item, piece of wood, metal, etc.) |
| | Flint | Strike a stone against another held stationary |
| | Flint in mouth | Strike a stone against another held in mouth |
| | Pound on surface | Pound a stone on a substrate |
| | Rub in mouth | Rub a stone against another held in mouth |
| | Rub/roll on surface | Rub or roll a stone on a substrate |
| | Rub stones together | Rub stones together |

| | | |
|---|---|---|
| | Rub with mouth | Rub a surface with a stone held in mouth |
| | Scatter | Scatter stones about, on a substrate, in front of oneself |
| | Shake in hands | Take stones in one’s open palm hand and shake the stones with the hand moving back and forth |
| | Slap | Slap, tap or pound a stone with one’s fingertips or palm of hand |
| | Swipe | Swipe stones together (both hands moving in a sweeping gesture) |
| | Tap in mouth | Tap a stone held in mouth with fingertips or palm of hand |
| Other complex manipulative activities | Flip | Turn a stone over with both hands |
| | Put in water | Put a stone in water |
| | Roll in hands | Roll a stone in one’s hands |
| | Rub/put on fur | Rub or put a stone on one’s fur while self-grooming |
| | Rub with hands | Hold a stone in one hand and rub it with the other (like potato-washing) |
| | Spin | Spin a stone around on the ground using two fingers of one hand or both hands (one moving forward and the other backward) |
| | Stone-groom | Allo-groom with a stone |
| | Throw | Throw a stone without jumping or running |
| | Throw and jump | Throw a stone and jump (or vice versa) |
| | Throw and run | Throw a stone and run (or vice versa) |
| | Throw and sway | Throw a stone and sway (or vice versa) |
| | Wash | Put a stone in water or pick up a stone from water and rub it with hands |
| | Wrap in leaf | Wrap a stone in a leaf (or wrap a leaf around a stone) |

*Source:* After Leca et al. (2007a)

**Fig. 9.2** *Glance-6476* (3-year-old, middle-ranking female): first individual recognized to perform SH on December 7, 1979

observation that SH was not likely innovated earlier than 1978 or 1979, as otherwise we should expect to have found older stone handlers during these early surveys. Eleven years on into the study in 1991, every individual under the age of 10 was observed to SH. Thus, in contrast to other examples of cultural behavior reported in Japanese macaques, SH first spread laterally among young individuals of the same age, and only began to be transmitted from adults to offspring when the first female stone handlers began to have offspring of their own.

The route of transmission of a novel behavior is in part determined by the nature of the behavior and the social networks in which it normally occurs. Those individuals most likely to be together while engaging in a particular kind of behavior, whether it be play, foraging, grooming, or sleeping, should be more likely to learn variants of these behaviors from one another (Huffman 1996).

## 9.4 Environmental Versus Social Influences of a Demonstrator, and the Role of Developmental Constraints in the Acquisition and Expression of Stone Handling

The long-term study at Arashiyama allowed us to determine the general pathways of diffusion of SH and evaluate the factors that may have contributed to the spread of SH within the group. On the one hand, mothers were presumed to be the primary source of an infant's early exposure to SH (Huffman 1984, 1996). On the other hand, we believe that there are atypical environmental conditions, such as the concomitant presence of provisioned foods and numerous stones, sometimes artificially brought by humans around the open space of feeding sites, under which the innovation and initial diffusion of SH could be facilitated (Huffman 1996; Leca et al. 2008a; Nahallage and Huffman 2008a,b).

However, only through controlled captive conditions are we able to systematically evaluate the possible contributions of environmental, social, and developmental factors to behavioral acquisition. Nahallage and Huffman (2007b) studied the SH behavior of a captive group of 48 Japanese macaques at the Primate Research Institute, Kyoto University, for 24 months spanning two breeding seasons between 2003 and 2005, during which 14 infants were born.

### *9.4.1 Environmental Factors*

Based on a detailed analysis on the exposure of infants to specific areas of an outdoor enclosure with varying stone availability, we failed to validate the environmental stimuli hypothesis, which states that the total time spent in areas with high stone availability and, therefore, exposure to more stones increases the likelihood that an infant will acquire SH behavior. We found no significant correlations between the age of SH acquisition and the rate of stones encountered from birth to acquisition of the behavior.

### *9.4.2 Access to Demonstrators by Naïve Individuals and the Acquisition of Behaviors*

We investigated the effect of pivotal individuals as demonstrators on the initial acquisition and development of SH behavior by focusing on interindividual interactions, in particular, mother–infant dyads. In the 14 mother–infant dyads born during the study, all but one infant started SH within the first 6 months after birth. There was great variability among them in the age SH was first displayed (6–31 weeks). During their first 3 months of life, infants spent 75% of the time within 1 m of their mother, significantly more time than they spent with other individuals. This high level of proximity to the mother had a significant impact on the age at which SH was acquired. Infants of mothers with higher SH frequencies exhibit the behavior earlier than infants of less frequent SH mothers. Two infants who were born in consecutive years to the same non-SH mother were the last to acquire the behavior. These results suggest that the acquisition of SH behavior in infants was strongly influenced by the amount of time spent in proximity to a stone handler and the frequency of the behavior displayed by that model (Nahallage and Huffman 2007b). Infants of frequent SH mothers spent proportionally twice as much time (83%) watching their mothers when she was SH than did infants whose mothers showed low SH frequency (42%). The former tried to take stones away from their mothers in 75% of the SH bouts whereas the latter tried to do so in only 33% of these bouts, resulting in a difference in the amount of time an infant took part in its mother's activity. Differences in a mother's SH frequency could affect their infant's exposure to SH, opportunities to handle stones, and practice SH.

### 9.4.3 Constraints of Neuromotor Development on the Expression of SH Behaviors

Few longitudinal studies have been conducted on the ontogeny of specific cultural behaviors; rather, most tend to deduce development from cross-sectional observations (Lonsdorf 2005). Furthermore, neuromotor development has rarely been considered as a constraint in the expression of matched behavioral patterns between experienced and naïve individuals. Our study showed that although mothers had a strong influence on the initial acquisition of SH behavior in infants, infants did not perform the same behavioral patterns as adults mainly because of developmental constraints in the kinds of behaviors they could perform (Nahallage and Huffman 2007b). There was a gradual increase in the number and complexity of SH patterns displayed by infants, which revealed a neuromotor developmental phase of this behavior. The infants we studied acquired the basic SH behaviors at around 2 to 3 months. Common to other behavioral traits observed during the early stages of infant development in macaques, stone manipulation patterns were quite simple actions, mainly, pick up, cuddle, lick, or bite a stone, and typically short in duration. Infants did not perform any complex manipulative action with stones during this time. The average number of patterns performed by an individual up to 6 months of age was 3.75 ± 1.90. At around 6 months, individuals started to perform more complex stone-directed actions such as clacking or rubbing two stones together or on a substrate. On average, they displayed 8.85 ± 2.26 patterns from 6 to 12 months of age. According to neuromotor studies on macaques, the earliest sign of relative independent finger movement (RIFM) occurred at 2 to 3 months, with mature patterns occurring at 7 to 8 months (Bortoff and Strick 1993). Galea and Darian-Smith (1995) reported that performance on a reach-and-grasp test by a group of young macaques approached adult levels by 6 months. This finding agrees with our study showing infants starting the behavior between 2 and 3 months and performing activities that require firm grasp of the stones around 6 months. Even though the neuromotor projections responsible for finger movement develop rapidly in the first neonatal months, they do not mature until the second year of life; this explains the increase in the number of SH patterns up to 3 to 4 years of age. Older juveniles displayed the highest number of patterns among all age classes (18.14 ± 5.38), whereas the number of patterns displayed decreased into adulthood, which might reveal the appearance of individual preferences or behavioral routines over the years (Nahallage and Huffman 2007b).

We concluded that, at the time of acquisition, infants acquired a rudimentary form of SH, but were constrained from matching specific behaviors from the demonstrator because of their level of neuromotor development. Our findings support developmental theories on juvenile primates (Pereira and Fairbanks 1993).

Later on, however, this kind of matching did occur, and was particularly noticeable for rare behaviors displayed by the mother, which were then being seen to diffuse among offspring and others. A good example for this is the throw-and-run behavior displayed by the alpha female of the group. Her son first started throwing stones when he was 1.5 years old but was not able to perform the run and throwing together, but by around 3 years of age he was seen performing the throw-and-run behavior just like his mother. They were the only individuals who displayed this behavior in the group (Nahallage and Huffman 2007b; Leca et al. 2008c).

## 9.5 Exploring and Explaining Intergroup Behavioral Differences

### *9.5.1 The Method of Elimination*

Recently, primatologists have found evidence of intergroup behavioral variation in several nonhuman primate taxa including capuchins, macaques, and great apes (Whiten et al. 1999; Huffman and Hirata 2003; Perry et al. 2003; van Schaik et al. 2003b; Leca et al. 2007a). The "method of elimination" is a multistep decision procedure that may be used to assess whether a geographically variable behavior is or is not traditional or cultural (van Schaik 2003; see also Boesch 1996).

First, a patchy geographical distribution of the behavior must be demonstrated. Within the same (sub)species, a given behavioral pattern can be customary or at least habitual in some groups and rare or even absent in others although it is ecologically possible. Similar to some ethnographic research in human social sciences or the powerful comparative method used in ethology, this group-contrast approach to cultural primatology has been widely used by field primatologists as a first step to identify candidates for cultural behaviors, particularly in primate stone-tool cultures (Whiten et al. 1999).

Second, intergroup behavioral differences are typically attributed to genetic, environmental, or cultural factors (Goldberg and Wrangham 1997; Whiten et al. 1999; Yamakoshi 2001). By elimination, when obvious genetic and ecological causations can be ruled out, or at least when the effects of genetic and ecological factors are likely to be minimal, then intergroup behavioral variation is largely considered cultural.

Third, the behavior should meet a set of criteria, such as being observed in at least two members of one group, showing pathways of diffusion within age structures, affiliated networks, or along matrilineages, being largely dependent on social means for its diffusion and maintenance, and being persistent across generations or at least over a number of years (Fragaszy and Perry 2003). As more elements congruent with the concept of tradition are provided, the likelihood of alternative interpretations decreases (van Schaik 2003). Accordingly, if a behavior shows a geographically patchy distribution unlikely attributable to genetic or ecological differences between sites, and if it is long lasting and socially transmitted, then a cultural phenomenon can be inferred (McGrew 2003).

### 9.5.2 Exploring Genetic, Ecological, Demographic, and Social Factors

To better understand how the SH tradition in Japanese macaques may appear, spread, and be maintained within the group over generations, we used the method of elimination to investigate the roles of genetic, ecological, demographic, and social factors in explaining intergroup similarities and differences in SH (Leca et al. 2007a,b, 2008a,b,c). Our main goal was to test several hypotheses proposing that SH variability reflects more demographic and social constraints than genetic and ecological factors. Our specific objectives were (1) to establish the comprehensive repertoire of SH local variants in Japanese macaques; (2) to provide a systematic and broad intergroup comparison of the frequency, form, and context of occurrence of SH; (3) to address the possible role of genetic determinants in SH variation, through a comparison of the behavior in the two subspecies of Japanese macaques, *M. fuscata fuscata*, widely distributed in the Japanese archipelago, and *M. fuscata yakui*, endemic to Yakushima Island, a small island at the southern limit of distribution of the species (cf. Fooden and Aimi 2005); (4) to evaluate three major environmentally based hypotheses invoked to account for intergroup differences in SH; (5) to consider the influence of various sociodemographic constraints on the appearance, diffusion, and maintenance of SH; (6) to test the association between geographical proximity and behavioral similarity as a way to infer a phenomenon of cultural zone; and (7) to explore the transformation over time in the form of SH from the perspective of stone-tool use in nonhuman primates.

We conducted a systematic comparison of SH in ten groups of Japanese macaques. Nine groups belonged to the *M. fuscata fuscata* subspecies and one group was *M. fuscata yakui* (see Chap. 2). Four captive groups were housed in large outdoor enclosures at the Kyoto University Primate Research Institute (PRI), and Japan Monkey Centre, Inuyama, and six free-ranging provisioned groups lived at four geographically isolated sites in Japan, namely, Arashiyama, Takasakiyama, Koshima Islet, and Shodoshima Island (Fig. 9.3). The comparison represented a total of 2,328 individuals and included two long-term studied groups at Arashiyama and Takasakiyama. We used the same observation procedure in all groups studied: continuous focal-animal sampling interspersed with instantaneous group scan sampling, and occasionally supplemented with ad libitum sampling (Altmann 1974). We analyzed a total of 1,950 h of observation, including 1,280 video-recorded SH bouts (Leca et al. 2007a). We provided a rigorous documentation of the local environmental context of SH occurrence, such as site-specific stone availability and the conditions of food provisioning (Leca et al. 2008a,b).

### 9.5.3 Intergroup Variation in SH

We listed a total of 45 different behavioral patterns in the SH repertoire of Japanese macaques (Leca et al. 2007a; Nahallage and Huffman 2007a). By taking a

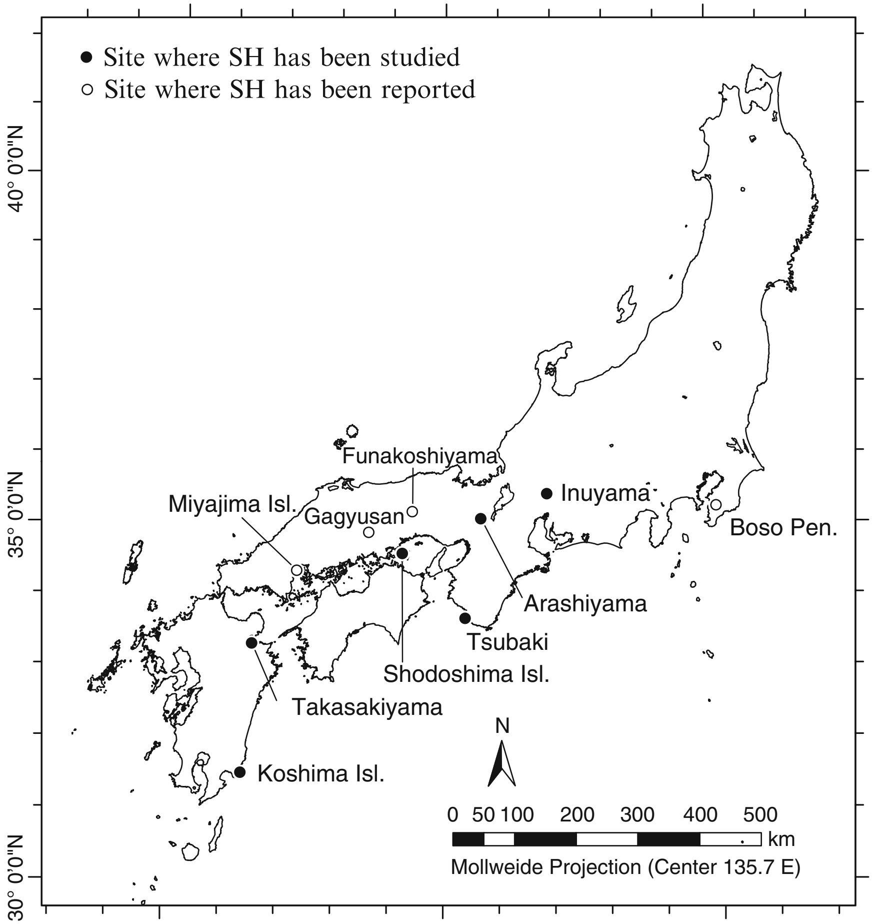

**Fig. 9.3** Map of the sites in Japan where SH has been studied or reported. [*Sources:* Arashiyama, Funakoshiyama, Gagyusan, Boso Peninsula, Takasakiyama, Yakushima (Huffman and Hirata 2003); Arashiyama, Inuyama (Primate Research Institute and "Monkey Valley" at Japan Monkey Centre); Koshima, Shodoshima, Takasakiyama (Leca et al. 2007a); Tsubaki (Leca, unpublished data); Miyajima (Watanabe, personal communication). The base map is originated from "Boundary data of cities, towns and villages of Japan ver. 6.2," by ESRI Japan Corporation, with permission]

group-contrast approach to chart intergroup diversity in SH, Leca et al. (2007a) showed substantial variability in the frequency of occurrence and form of SH among the ten study groups. We found major intergroup differences in the frequency of occurrence and the prevalence of most of the 45 SH patterns, with local variants being customary in some groups, and rare or even absent in others although they were ecologically possible, and performed by a majority of individuals in some groups or only idiosyncratically in others (Leca et al. 2007a,b; see Table 9.2 for definitions).

**Table 9.2** Frequency of occurrence of the 33 SH patterns that are not observed in all the ten studied troops of Japanese macaques, four captive (PRI Arashiyama = Ara.A, Wakasa = Wak.A, Takahama = Takh., and Japan Monkey Centre = JMC) and six free-ranging troops (Koshima = Kosh., Arashiyama E = Ara.E, Shodoshima = Sho.A and Sho.B, Takasakiyama = Tak.B and Tak.C)

| | Captive troops | | | | Free-ranging provisioned troops | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| SH pattern | Ara.A | Wak.A | Takh. | JMC* | Kosh. | Ara.E | Sho.A | Sho.B | Tak.B | Tak.C |
| *Investigative activities* | | | | | | | | | | |
| Lick | P | H | C | P | P | P | (–) | (–) | P | P |
| Move inside mouth | – | H | H | P | – | P | (–) | (–) | P | P |
| Pick | C | P | P | P | P | P | P | (–) | (–) | P |
| Put in mouth | P | H | H | P | – | P | H | P | P | P |
| *Locomotion activities* | | | | | | | | | | |
| Carry | – | C | H | H | P | C | H | H | H | H |
| Carry in mouth | – | H | C | P | – | P | P | P | P | P |
| Move and push/pull | – | C | H | P | P | H | P | P | P | P |
| Toss walk | P | P | C | P | – | H | (–) | (–) | P | P |
| *Collection (gathering) activities* | | | | | | | | | | |
| Pick and drop | – | – | P | – | – | P | P | (–) | P | H |
| Pick up small stones | – | – | H | – | – | H | (–) | (–) | P | P |
| *Percussive or rubbing sound-producing activities* | | | | | | | | | | |
| Clack | P | P | H | H | – | – | P | P | P | P |
| Combine with object | – | P | C | P | – | H | (–) | P | (–) | P |
| Flint | – | H | C | P | – | P | P | P | P | H |
| Flint in mouth | – | P | P | – | – | – | (–) | (–) | (–) | P |
| Pound on surface | – | P | H | H | – | P | P | (–) | (–) | H |
| Rub in mouth | – | P | P | – | – | – | (–) | (–) | (–) | P |
| Rub stones together | – | H | C | P | – | C | P | P | H | H |
| Rub with mouth | – | P | P | – | – | – | (–) | (–) | (–) | (–) |
| Shake in hands | – | – | P | P | – | P | (–) | P | P | P |
| Slap | – | – | H | P | – | – | (–) | (–) | (–) | (–) |
| Swipe | – | P | P | – | – | P | (–) | (–) | P | H |

| | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| Tap in mouth | – | – | P | – | – | – | (–) | (–) | (–) | (–) |
| *Other complex manipulative activities* | | | | | | | | | | |
| Flip | – | P | H | – | – | P | (–) | (–) | P | (–) |
| Put in water | – | – | P | – | – | P | (–) | (–) | (–) | (–) |
| Rub/put on fur | – | H | P | P | – | P | (–) | P | (–) | (–) |
| Spin | – | – | P | – | – | – | (–) | (–) | (–) | (–) |
| Stone-groom | – | – | – | – | – | – | P | (–) | (–) | (–) |
| Throw | – | P | P | P | – | – | (–) | (–) | (–) | (–) |
| Throw and jump | – | – | H | – | – | – | (–) | (–) | (–) | (–) |
| Throw and run | – | – | P | P | – | – | (–) | (–) | (–) | (–) |
| Throw and sway | – | – | P | – | – | – | (–) | (–) | (–) | (–) |
| Wash | – | – | P | P | – | H | (–) | (–) | (–) | (–) |
| Wrap in leaf | – | – | H | – | – | – | (–) | (–) | (–) | (–) |
| No. of pattern occurrence | 5 | 20 | 32 | 19 | 4 | 20 | 11 | 10 | 15 | 19 |

No asterisks, *Macaca fuscata fuscata* troops; asterisk, *M. f. yakui* troop; neighboring troops living at the same site (respectively, two troops at Shodoshima and two troops at Takasakiyama)

C, customary: exhibited by at least 90% of the sampled individuals in at least one age class, or at least 70% of the sampled individuals in at least two age classes; H, habitual: not customary but observed at least three times in several individuals, consistent with some degree of social transmission; P, Present: not customary or habitual, but observed at least once; –, absent: not observed despite sufficient observation time (at least 90 h of total observation time); (–), unknown: not observed but absence uncertain because of insufficient observation time (less than 90 h of total observation time); no. of pattern occurrence, number of SH patterns scoring at least the present status

The frequency of occurrence of SH patterns was highly variable according to the pattern and group in question. Very few patterns were unique to any group, as most were shared between two or more groups. Even though most simple SH patterns (corresponding to investigative, locomotion, and collection activities) could be observed in most study groups, their frequency of occurrence varied from being present or to being a customary practice. The frequent occurrence of more complex SH patterns (*flint*, *combine with object*), corresponding to percussive, rubbing, and other complex manipulative activities, was even more restricted to particular groups, but again highly variable depending on the pattern. Finally, a few complex SH patterns were specific to one group, such as *tap in mouth*, *spin*, and *wrap in leaf* in the Takahama group, and *stone-groom* in the Shodoshima A group.

Following Whiten (2005), we defined a "tradition" as a local behavioral variant, showing different frequencies of occurrence across the study sites, that is, being customary or habitual in at least one site but absent elsewhere. We defined a "culture" as a package of multiple related traditions, and "cultures" as distinctive arrays of clustered traditions. Almost all SH patterns showed geographically patchy distributions, that is, had different profiles of frequency of occurrence across the study sites, and were referred to as local variants or SH traditions. In terms of behavioral complexity, we found three levels of SH culture, each level being defined by group-dependent clusters of SH traditions (Leca et al. 2007a).

In summary, our results revealed a significant intergroup variability in the form of SH, consistent with the extensive and multiple intersite behavioral differences recorded in chimpanzees, and interpreted as cultural variation (cf. Whiten et al. 1999).

### *9.5.4 No Major Evidence for Genetic Determinants in SH Variation*

First, our comparative study revealed that *M. fuscata yakui* did not notably differ from *M. fuscata fuscata* in the SH repertoire, as well as in the occurrence, form, and context of SH. We found that SH patterns varied as much among seven groups of the same subspecies (*M. fuscata fuscata* in Wak.A, Takh., Ara.E, Sho.A, Sho.B, Tak.B, and Tak.C) as between subspecies themselves (*M. fuscata fuscata* versus *M. fuscata yakui*; Leca et al. 2007a).

Second, the occurrence of SH behavior in rhesus macaques (*Macaca mulatta*) and long-tailed macaques (*M. fascicularis*) confirmed the prediction that closely related macaque species shared a behavioral propensity for SH (Huffman and Hirata 2003; Nahallage and Huffman 2008a). With the exception of one variant, all the SH patterns displayed by the rhesus macaques were typical of Japanese macaques. We found no compelling evidence to suggest that the observed differences could be attributed to differences inherent to these two species (Nahallage and Huffman 2008a). Therefore, we can assume that most SH patterns are macaque "universals." All the basic motor actions involved in every SH pattern are shared behavioral predispositions; that is, they are already present in the repertoire of the genus *Macaca* (Huffman and Hirata 2003; Nahallage and Huffman 2008a).

Third, Fooden and Aimi (2005) provided information about the geographical distribution of extant populations of Japanese macaques, including continuities and discontinuities, migration, and genetic variability. There was evidence for geographical variation in mitochondrial DNA of Japanese macaques (Hayasaka et al. 1991). Although it is acknowledged that genes determine the occurrence of general behavioral categories within a given species, such as the ability to handle stones or use tools, we suggest that intraspecific genetic differences are negligible in terms of possible implications for local behavioral variants, such as the manual dexterity to clack stones rather than rub the stones together.

In sum, based on comparative analyses at the subspecies and species levels, common behavioral predispositions in phylogenetically close taxa, and knowledge of genetic determinism, it is reasonable to consider that genetic and phylogenetic factors may not be key to explaining the observed intergroup variability in the form of SH in macaques (Leca et al. 2007a; Nahallage and Huffman 2008a).

## *9.5.5 Role of Ecological Factors in SH Variation Between Groups*

SH is a behavior particularly well suited for the method of elimination. Its apparent lack of direct adaptive consequences and the arbitrariness of its behavioral variants make it easier to rule out ecological factors as potential causes of intergroup variation (Leca et al. 2008b). Among the most obvious ecological differences that could affect SH, we addressed site-specific availability in stone number and size, the degree of terrestriality of individuals, and food provisioning constraints.

### 9.5.5.1 Stone Availability and Terrestriality

Although we demonstrated that SH is almost exclusively a terrestrial activity, our comparative analyses showed that the number of stones readily available and the relative amount of time spent on the ground by the macaques were not significantly associated with the intergroup differences in the occurrence of SH. Moreover, the size of stones handled was not associated with the size of stones available (Leca et al. 2008b). The absence of evidence supporting the stone availability and terrestriality hypotheses suggests that the performance of SH and the motivation to engage in this activity are both more diverse and more complex than the direct links to time spent on the ground or the number of stones readily available in the local environment.

However, this finding does not imply that any dramatic local change in the availability of stones or substrates (such as vertical structures) would not affect the chance of SH to occur or the form of SH in a particular group. We believe that there are favorable environmental circumstances under which the innovation and initial diffusion of SH could be facilitated (Leca et al. 2008a; Nahallage and Huffman 2008a,b).

#### 9.5.5.2 Food Provisioning

Food provisioning undoubtedly affects the animals' activity budget (Huffman 1991; Huffman and Hirata 2003; Leca et al. 2008a; Jaman and Huffman 2008). Feeding macaques gives them "free" time because they can devote less time to foraging. Moreover, attracting macaques to the open space of feeding sites, where stones occur and many individuals can gather and observe each other, may result in increased behavioral coordination at the group level and contagion-like processes. In this context, the occurrence of an individual starting to manipulate stones could enhance the probability for a neighboring group member to exhibit SH. In turn, the latter stone handler could enhance the probability for another neighboring group member to exhibit SH, and so on. Therefore, food provisioning is likely to increase the chances for SH to emerge and diffuse, or at least to be expressed.

We found that food provisioning constraints, including provisioning frequency, duration of food availability, and the size of food items, considerably influenced a group's food-related activities and feeding style, which in turn could affect several aspects of SH. In groups provisioned several times a day, SH was more frequent, lasted longer, and was more prevalent during provisioning than nonprovisioning periods. These effects of provisioning were not significant in groups provisioned less frequently. Moreover, SH was more frequently integrated with food-related activities in groups supplied with food several times a day than in the other groups. Thus, we argued that the context of occurrence, frequency, and form of SH in a given group were directly influenced by provisioning parameters (Leca et al. 2008a). Food provisioning may be a key factor in the innovation and transformation phases of the SH tradition in Japanese macaques. However, evidence for relationships between SH and food provisioning does not argue against a cultural interpretation of SH, as this long-enduring behavior is socially transmitted (Huffman 1984, 1996; Nahallage and Huffman 2007b), which some authors suggest is sufficient evidence of a behavioral tradition (Perry and Manson 2003).

### *9.5.6 Demographic Constraints on the Emergence, Transmission, and Maintenance of SH*

By both facilitating and limiting the expression of particular behaviors, demographic factors may influence the likelihood of individual innovation, the subsequent diffusion of a novel behavior within a group, and its long-term maintenance (Huffman and Hirata 2003). Group size and composition can be regarded as major constraints to the appearance, spread, and transformations over time of traditional behaviors. Here, we evaluated how group size, and the age structure of the group, may account for the substantial intergroup variations in SH reported in Japanese macaques.

The ten study groups varied greatly both in size and in proportion of individuals belonging to the different age classes (Leca et al. 2007b).

#### 9.5.6.1 Group Size

We found that group size was positively correlated with the percentage of group members exhibiting SH simultaneously. The larger the group, the higher the proportion of individuals performing SH at the same time (Leca et al. 2007b). The effect of group size on the synchronized performance of SH may reveal the contagious nature of play. Seeing group members playing is a reliable cue for more individuals that the current environmental conditions are safe enough to engage in play. The sight of nearby stone handlers and even the loud noise generated by percussive patterns may increase the individual probability to start handling stones. This stimulation effect may be amplified by an increasing number of group members and eventually result in a form of “hysterical contagion.” This finding may help to explain the increase in number of SH individuals (synchronized occurrence) around feeding time in free-ranging provisioned groups, as this is the only time when most group members are all together in the same location.

#### 9.5.6.2 Age Structure

Another demographic factor, age-class composition of the group, may also affect the diffusion and maintenance of SH. We verified that a group with abnormal age structure (e.g., missing age classes) showed a lower proportion of stone handlers and lower frequency of SH than more normally age-structured groups. The very low occurrence and frequency of SH in the captive Arashiyama A group, with no subadults and young adults, strongly supported the view that a group’s age structure might affect the diffusion and maintenance of SH behavior. We suggested that the age gap in the Arashiyama A group might have constrained the diffusion of SH from the young to the older group members (Leca et al. 2007b). The restricted practice of SH by young individuals and only very occasional practice by older group members may not be sufficient to maintain the behavior in this group in the long term.

These findings are consistent with long-term field observations conducted at Arashiyama and described earlier, suggesting that (1) after initial innovation by youngsters, SH behavior first spreads among young individuals, probably peer-playmates; (2) there is a critical period after which SH cannot be acquired by an individual (>5 years of age); and (3) when a behavioral practice is restricted to a particular class of group members, its propagation should be slow and its maintenance may be jeopardized (Huffman 1996; Leca et al. 2007b,c, 2010b).

In sum, the present findings supported the hypothesis that patterns of variation in SH across groups reflected variability in group size and composition in age classes.

## *9.5.7 Social Influences and Observational Learning in SH*

### 9.5.7.1 Cultural Zones

We found a positive correlation between geographical proximity and cultural similarity in SH between groups. In other words, there were significantly greater similarities in SH patterns in the groups living at the same site, compared to other groups. The numbers of patterns showing the same occurrence in the two groups living at Shodoshima (Sho.A and Sho.B) and in the two groups living at Takasakiyama (Tak.B and Tak.C) were 25 and 24, of 33, respectively (see Table 9.2). These neighboring groups had similar sets of SH patterns, and their total numbers of patterns observed were close (23 and 22 at Shodoshima, and 27 and 31 at Takasakiyama; Leca et al. 2007a).

The geographical distribution of clear group-dependent clusters of SH variants and the similarities in the SH repertoires between the free-ranging groups living at the same site were suggestive of the phenomenon of cultural zones, because any alternative explanation is hard to imagine. Although food provisioning schedules were different, neighboring groups had overlapping home ranges and came into occasional contact around the provisioning site, where SH activity most often occurs.

The notion of cultural zones is based on the possibility of (1) intergroup observation when macaques come into occasional contact around the feeding sites where most SH activity occurs and (2) males transferring SH patterns when migrating from one group to another. When such intergroup social influences do not exist (e.g., groups separated by substantial geographical distance in natural situations or by artificial barriers such as concrete walls in captive conditions), the groups showed more differences in their SH repertoires: their mean number of behaviors showing the same frequency of occurrence was only 12.1 ± 7.3. Intergroup cultural transmission in wild chimpanzees has been inferred from the geographical distribution of certain tool-using behaviors and social conventions (Boesch et al. 1994; McGrew et al. 1997, 2001), and suggested from field experiments (Biro et al. 2003).

In Japanese macaques, food provisioning provokes, several times a day, the gathering of most group members around feeding sites. Attracting macaques to the open space of feeding sites, where small-sized foods (cereal grains) are scattered on the ground among stones, increases considerably their chances to encounter these objects, and spatial proximity among individuals represents opportunities to observe others handling stones. Although SH is a primarily solitary activity, non-SH individuals are very likely to observe performances of SH by other group members and often show close interest in others' stones (Huffman and Quiatt 1986; Quiatt and Huffman 1993; Leca et al. 2008b).

### 9.5.7.2 Social Tolerance and Spatial Cohesion

To test the hypothesis that SH will be more prevalent in more cohesive groups, we calculated, for the ten study groups, a group-level index of social tolerance, defined as the mean percentage of group members within 1 m of each other. This typical index of group-level social tolerance was not significantly correlated with the frequency and rate of diffusion of SH (Leca, unpublished data). In other words, the groups showing higher levels of positive social interactions (such as grooming and playing) were not necessarily the groups with more frequent episodes of SH and higher percentages of stone handlers. Instead, group size and group spatial cohesion after food provisioning was positively correlated with the prevalence of SH. Larger groups characterized by closer physical proximity among individuals feeding on provisioned food also showed higher percentages of group members exhibiting SH simultaneously (Leca et al. 2007b).

Therefore, intergroup differences in SH prevalence and cultural similarity in SH between neighboring groups were better explained by intergroup transfers, as well as opportunities for observational learning and behavioral coordination both within and between groups rather than intragroup social tolerance alone.

#### 9.5.7.3 Transformation of the SH Tradition

The transformation phase of the SH tradition is defined as the late period in which long-enduring practice and acquired familiarity with the behavior and the stones are gained through the integration of SH with other daily activities (Huffman and Quiatt 1986; Huffman and Hirata 2003). By using similar methods of data collection for about 15 years of continued observation at Arashiyama and Takasakiyama, we found that the macaques have almost doubled the size of their SH repertoire and largely diversified the contexts in which SH activity was practiced (Leca et al. 2007a).

We expect such an increase over time in the number and diversity of SH patterns to be found in other groups where the SH tradition is well established. Based on data from Arashiyama and Takasakiyama, we also expect to find in other groups a cumulative increase in the complexity of the SH repertoire, from simple SH patterns observed in the first year following the appearance of the behavior within the group, to more complex SH patterns performed after several years of daily practice of the behavior at the group level.

The late emergence of SH patterns not recorded before involved complex manipulative actions, such as *combine with object*, *rub/put on fur*, *stone-groom*, and *wash* revealed an increased diversity in the combination of stones with other objects or substrates. The appearance of variants combining the use of hands and mouth (e.g., *carry in mouth*, *move inside mouth*, *bite*, and *lick*) suggested that SH had become more integrated with foraging and feeding activities. The integration of SH with food-related activities and the emergence of food-directed SH patterns were more frequent in free-ranging groups where food provisioning strongly influenced the activity budget.

In human material culture, the “ratchet effect” is referred to as the cumulative modifications and incremental improvements resulting in increasingly elaborate technologies (Tomasello 1999). Our longitudinal data suggested that the long-term cultural transformation of SH might result in a generational ratchet effect, defined as an increase in the diversity and complexity of SH patterns compared to earlier generations of stone handlers.

From a functional point of view, almost all the 45 SH patterns currently observed in Japanese macaques are regarded as a noninstrumental manipulation of stones, with no obvious survival value (Huffman 1984; Leca et al. 2007a; but see Nahallage and Huffman 2007a for a possible ultimate function of SH). When combined with other objects, the stones handled by Japanese macaques were never used as tools to achieve an overt goal.

However, when practiced on a daily basis and by most members of a group, the noninstrumental manipulation of stones could be considered as a behavioral precursor to the possible use of stones as tools (Huffman and Quiatt 1986; Huffman 1996; Leca et al. 2008a). The gradual transformation of the SH tradition, associated with a generational "ratchet effect," could ultimately result in future stone-tool use, as stone-related behaviors become more deeply ingrained into the behavioral landscape of these macaques at the population level. For example, the persistence of SH in food-related contexts may eventually turn into the instrumental use of stones as foraging tools by Japanese macaques (Huffman and Quiatt 1986; Leca et al. 2008a).

This prediction was eventually verified. Until recently, there was no optimal SH pattern and no local survival advantage in performing a particular SH pattern rather than another. However in 2004, we witnessed the emergence of the first example of a possible adaptive transformation in the spontaneous practice of SH. In contrast to all other SH patterns performed by Japanese macaques, unaimed stone-throwing was exclusively observed in the captive Takahama group during periods of disturbance, and in conjunction with agonistic signals typical of this species could be regarded as a spontaneous tool-using behavior (Leca et al. 2008c). Based on the analysis of the contexts that may elicit the behavior, we inferred that stone-throwing might serve to augment the effect of agonistic displays. The Takahama group was the only one to show a complexity level-3 SH culture. This group also exhibited the most diverse SH repertoire (44 patterns of a total of 45) and showed the highest frequencies of occurrence in SH patterns (28 habitual or customary patterns) among all groups. These findings suggest that, although SH was observed in the ten studied groups, the transformation of SH into an adaptive behavior is more likely in groups where SH is a well-established behavioral tradition showing diverse and complex patterns performed in various contexts.

This study of stone-throwing also supports the view that tool-use evolves in stages from initially nonfunctional behaviors, such as object play (Beck 1980; Huffman and Quiatt 1986; Leca et al. 2008c), a categorization that perfectly suits the SH activity (Huffman 1984). Food provisioning and captivity have relaxed selective pressures on foraging and created favorable environmental conditions under which SH may simply serve the function of maintaining in some populations a set of behaviors that could evolve into tool-use provided particular environmental circumstances exist. As an unselected but eventually beneficial trait, the SH tradition would be an exaptation (cf. Gould and Vrba 1982).

### *9.5.8 Possible Functions of Stone Handling Behavior*

Although not every socially learned behavior needs to be adaptive, the propensity to learn and adopt new behaviors certainly is. In the immediate sense, SH appears to be rewarding in itself, rather than the means to an end (Huffman 1996). Why the behavior persists in groups over many generations, despite the lack of any obvious direct adaptive value or function to those who practice SH, has long been an elusive question.

Two hypotheses regarding the occurrence of other types of object play in animals are the misdirected foraging behavior hypothesis and the motor training hypothesis. According to the misdirected foraging hypothesis, play in captive or domesticated animals is motivationally directed to objects as if they were food (Pellis 1991; Hall 1998; Pellis et al. 1988). However, SH as described here is not consistent with the misdirected foraging behavior hypothesis (pseudo-feeding behavior) proposed by Pellis (1991). Even in provisioned groups, SH occurs predominantly after feeding, not before. Thereby we conclude that this behavior is not elicited by the anticipation of food as described for captive otters and other zoo animals (Hediger 1964; Pellis 1991).

Although many theories have been proposed for the function of play behavior (Smith 1978), no single one can be applied across the board to all play behaviors in all species. Indeed, there are differences of play activities exhibited by the same species living under different environmental conditions (Ramsey and McGrew 2005). SH is no exception, as evidenced by the contrasts and similarities of the behavior between free-ranging and captive groups, and age-class differences within the same group reported here.

The underlying function of play is expected to vary according to the content of the behavior itself, potential motivational differences brought about by differences in the social and natural environment, and by species-level characteristics. This expectation is confirmed for Takahama macaques also, in that the frequency of SH is significantly greater on clear sunny days versus cloudy or rainy days as well as during warmer seasons of the year than in the colder months, and that macaques suppress SH for days following periods of externally induced intense stress, such as capturing the entire group for annual checkups, or moving a group temporarily into a new enclosure (Nahallage and Huffman 2008b).

When we compare age-class differences in SH, the possible motivations for performing the behavior appear to be different for young and adults (Nahallage and Huffman 2007a). This distinction is of particular interest to us, given that the behavior is only acquired by individuals when young. This difference leads us to speculate that in contrast to other play behaviors that disappear from the repertoire of most primates when they reach adulthood, presumably because they no longer serve a function, biological and cultural selective forces may be acting on individuals who have acquired SH to maintain the practice throughout life.

The immediate motivation for young to handle stones, as any other form of object play, is most likely to be that it is intrinsically an enjoyable activity (Hall 1998). The young are naturally curious about what others are doing and have the desire to play with an object made "popular" by others' use of it (Huffman 1984). At the functional level, playing with stones allows them to develop and practice the interactive use of motor and perceptual skills that support physical and neurophysiological development. In macaques, a surge of synaptogenesis occurs roughly 2 months before birth and continues up to 3 years of age (Rakic et al. 1986; Bourgeois et al. 1994). The overall trend in the increasing complexity of SH behaviors (pattern and number of behaviors) over time from infancy into the juvenile period is consistent with this increase in neuromotor developmental activity. These findings are consistent with Fairbanks' (2000) model describing the heightened frequency of object manipulation in correlation with synaptic development in juvenile savanna monkeys (*Cercopithecus aethiops*) and rhesus macaques (Rakic et al. 1986). We believe that this model is the best functional explanation for SH in young Japanese macaques.

For adults, the immediate motivation to SH appears to be different from that of the young. With age, adults exhibit fewer bouts of longer duration, involving relatively more complex behavioral patterns than in the young (Nahallage and Huffman 2007a). Adults focus on these more demanding manipulative activities, with seemingly intense concentration. They carry stones to their individually preferred locations to handle them in an unhurried, seemingly "leisurely," manner. Sometimes older individuals sit nearby their preferred location, waiting for others to leave, before going there to handle the stones, and performed the behavior most often in the afternoon. We suggest that SH may allow adults to temporarily divert their attention away from the social interactive network of associations with others by concentrating on this solitary activity. As adults have already acquired the necessary motor skills during early life, we propose that the ultimate function of SH is also different from that of the young. However, an equally important neurophysiological benefit may be gained by them from its practice. As macaques grow older, a decline in memory and cognitive impairment and associated pathology (senile plaque, synapse loss) of the prefrontal cortex occurs (see Hof and Duan 2001 for a review). Recently, a number of clinical studies have shown the benefits for elderly humans in significantly reducing the risk of acquiring such disease through regular leisure activities involving concentrated mental activity (reading, playing board games, cards, and musical instruments; e.g., Verghese et al. 2003). It has been suggested that the mental exercise of such leisure activities may stimulate new neural growth around damaged parts of the brain caused by aging (Coyle 2003). A shift in the role of SH activity from neuromotor development when young to basic maintenance in adults and regeneration of neurophysiological pathways in aging adults may be the prominent functions behind the sustained practice of this seemingly nonadaptive behavior in macaques.

## 9.6 Conclusions and Future Directions

In Japanese macaques, the individual acquisition and expression of SH behavior, the appearance, diffusion, and maintenance of the SH culture, as well as intergroup variation in the frequency, form, and context of occurrence of SH, were better explained by neuromotor developmental constraints, sociodemographic factors (namely, group size, age structure, intergroup transfers, opportunities for observational learning in mother–infant dyads and among peer-playmates, and behavioral coordination at the group level), and environmental factors that were not stone related (food provisioning) than by genetic differences, stone availability, or terrestriality. We presented what may be the most extensive and systematic survey focused on the intra- and intergroup variability of a single type of behavior in macaques to date. Through the combination of the method of elimination, cross-sectional and longitudinal analyses, evidence for social transmission and durability of SH, and the view of behavioral predispositions, we drew an overall picture of rich cultural diversity in a particular type of object play behavior in Japanese macaques. Among the rare nonadaptive proposed traditional behaviors [see also "leaf-pile pulling" in chimpanzees (*Pan troglodytes*); Nishida and Wallauer 2003], SH is the most thoroughly documented.

To further explore the proximate causes of SH and the constraints on its propagation and long-term transformation, our findings call for experimental approaches (1) to test the strength of the connection between SH and feeding activities, (2) to assess the influence of the physical characteristics of the stones on stone selectivity, (3) to examine the effect of the contagion process on the synchronized performance of SH, (4) to investigate how visual and auditory stimulus enhancement may help trigger SH behavior at the individual level, and (5) to evaluate the distinct effects of various social learning processes, such as social enhancement, social facilitation, or imitation, on the individual acquisition of SH. Such experiments could involve, respectively: (1) the manipulation of the food provisioning schedule, (2) the introduction into the environment of new stones varying in size, shape, weight, and chemical properties, (3) the manipulation of size of subgroups from a social group held in captive conditions, (4) the setting up of particular stone arrangements, such as piles of stones, to simulate SH by-products and the playback of sounds produced during SH activity, and (5) the introduction of stones to semi-isolated individuals or into caged groups under the controlled conditions of captive settings.

Field studies on geographical variation in the occurrence of numerous behavioral patterns, supported by longitudinal and experimental investigations of whether and how these behaviors are socially learned, can provide extensive evidence for behavioral traditions in primates (Huffman et al. 2008).

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# Chapter 10: Interaction Between Male and Female Mating Strategies and Factors Affecting Reproductive Outcome

**Shiho Fujita**

## 10.1 Introduction

Japanese macaques (*Macaca fuscata*) have multimale–multifemale social groups, which provides for complex male and female mating strategies. According to the primate sexual selection theory, males fundamentally compete with rival males for access to females. Male mating strategies include direct male–male competition, sperm competition, and sneak copulation. On the other hand, females have a counterstrategy against male sexual coercion: extended receptivity, which functions to conceal the exact time of ovulation from males, and thus prevents individual males from monopolizing access to females. Female mating strategies include mate choice toward particular males, which brings a female or her offspring material and/or genetic benefits, and mating with multiple males to prevent infanticide through paternity confusion.

Although many hypotheses have been provided for mating strategies in primates from the point of view of ultimate level, empirical data, especially on intraspecific variation, are scarce. In this chapter, I review the mating strategies of both sexes and the interaction between them in Japanese macaques. Both males and females employ various mating strategies through the underlying mechanisms of intra- and intersex competition. I also compare mating patterns between populations by using data mainly from Arashiyama, Yakushima Island, and Kinkazan Island. Japanese macaques are widely distributed in various habitats from warm-temperate evergreen forests to cool-temperate deciduous forests (Yamagiwa and Hill 1998; see also Chap. 5), and thus ecological conditions, such as food availability, in each habitat may lead to variations in mating behavior patterns.

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## 10.2 Mating Strategies in Males

### *10.2.1 Male–Male Competition and Male Mating Tactics*

According to the sexual selection theory, most male mammals compete for access to females (for review, see Paul 2002). In Japanese macaques, dominant males are sometimes observed to aggressively interrupt the mating of lower-ranking males (Huffman 1987, 1991a) and to guard females from rival males by engaging in longer mounting series (Soltis 1999) (Fig. 10.1). On the other hand, lower-ranking group males and non-group males often engage in alternative mating tactics known as sneak copulation (Sprague 1991; Soltis et al. 1997a, 2000; Takahashi 2001; Matsubara 2003; Hayakawa 2007). Dominant males have relatively higher mating success during mating season (Inoue et al. 1991; Takahashi 2001; Matsubara 2003; Hayakawa 2007) although guarding females from rival males involves a high expenditure of time and energy. In contrast, mating of lower-ranking males depends on female proceptive behaviors and the available number of sexually receptive females (Matsubara 2003). Hence, dominant males seem to follow a "secure" strategy, whereas subordinate males follow a "chance" strategy (Inoue et al. 1991). In addition, because females copulate with multiple male partners during the fertile period (Soltis et al. 1999, 2001; Matsubara and Sprague 2004; Hayakawa 2007), males compete in not only the contest style but also the scramble style through sperm competition.

**Fig. 10.1** Mounting series is finished with the ejaculation pause (Kinkazan Island)

### *10.2.2 Association Between Male Dominance Rank and Reproductive Success*

The "priority of access" model predicts that dominant males should attain higher mating success and thus greater reproductive outcome (Altmann 1962). However, the number of females simultaneously in estrus constrains the capacity of a male to monopolize mating of all females and retain exclusivity of male mating access (Berenstain and Wade 1983). Females in seasonal breeding species, including Japanese macaques, are more likely than nonseasonal breeders to synchronize their estrus by chance, and, therefore, there is a weak association between male rank and reproductive success (Paul 1997, 2004).

Table 10.1 shows the effects of male dominance rank on mating success or reproductive success in some populations. In most cases, male dominance rank positively correlated with mating success. However, in the Wakasa group at the Primate Research Institute (PRI) in Kyoto University, dominance rank was highly correlated with mating success but not with reproductive success (Inoue et al. 1990, 1991, 1993). Similarly, at Yakushima, the correlation between dominance rank and mating success was higher than that between rank and reproductive success (Soltis 1999; Soltis et al. 2001). These findings suggest that observed mating overestimates the reproductive outcome of dominant males.

What factors other than dominance rank affect male reproductive success? First, the number of females in simultaneous estrus should affect the success of dominant males in monopolizing females. Dominant males can more easily guard females from rival males when fewer females are in estrus at the same time. For example, at Kinkazan, where the operational sex ratio (OSR, the number of estrous females per male) fluctuates from year to year, all group males had mating opportunities when the OSR was ≥1 (female-biased); in contrast, lower-ranking males had very few mating opportunities when the OSR was <1 (male-biased) (Takahashi 2004). In addition, when the OSR was <1, no mating of non-group males was observed, and group males monopolized successful mating inside the group (Takahashi 2001).

The ability of dominant males to monopolize mating with receptive females is reflected in their reproductive outcome. In the enclosed group at PRI, although male rank and reproductive success were not significantly correlated, the mean number of estrous females per day was 3.6, and the alpha male sired 23% (3/13) of the offspring (Soltis et al. 1999). Similarly, in the unprovisioned wild group at Yakushima, the mean number of estrous females per day was 2.4, and the alpha male sired 33% (2/6) of the offspring (Soltis et al. 2001). In this case, male rank has relatively high correlation with both mating success and reproductive success (Table 10.1). In such circumstances, dominant males could succeed in guarding some but not all of the females from rival males. In contrast, at Arashiyama, there was an average of 15.6 females on average per day, and none of the offspring was sired by the alpha male (Inoue and Takenaka 2007) (Table 10.1). In such a situation, female mate choice might dilute the effects of dominance rank on reproductive success because females sometimes prefer to mate with lower-ranking group males and non-group males (see following).

**Table 10.1** Association of dominance rank with mating and reproductive success

| Group<br>Condition<br>Years | Wakasa at PRI<br>Captive<br>1987–1991<br>(4 years) | Wakasa at PRI<br>Captive<br>1993–1994<br>(1 year) | Arashiyama B<br>Provisioned<br>1975–1977<br>(2 years) | Arashiayama E<br>Provisioned<br>2002–2003<br>(2 years) |
|---|---|---|---|---|
| Number of adult females | 18–24 | 21 | 74–84 | 93–100 |
| Number of adult group males | 9–10 | 8 | 21–35 | 24–27 |
| Number of non-group males[a] | 0 | 0 | 0–7 | Present |
| Socionomic sex ratio[b] | 0.41–0.50 | 0.38 | 0.25–0.37 | 0.24–0.29 |
| Mean number of estrous females per day | – | 3.59 | – | 15.6 |
| Correlation coefficient between male dominance rank and mating | 0.84 | n.s. | 0.893 | – |
| Correlation coefficient between male dominance rank and paternity | n.s. | n.s. | – | 0.402 |
| Percentage (ratio) of the offspring that an alpha male sired | 12.5 (1/8)[c] | 23.1 (3/13) | – | 0 (0/23) |
| References | (1) | (2) | (3) | (4) |

| Group | Yakushima<br>Nina-A | Yakushima<br>Nina-A | Yakushima B<br>Wild |
|---|---|---|---|
| Condition | Wild | Wild | 1996–1998 |
| Years | 1997–1999<br>(2 years) | 1999–2001<br>(2 years) | 1999–2000<br>(4 years) |
| Number of females | 12 | 6–7 | 2–7 |
| Number of group males | 15 | 7–10 | 0–7 |
| Number of non-group males[a] | 0 | 2–11 | 4–13 |
| Socionomic sex ratio[b] | 1.25 | 1.17–2.5 | 0–1.50 |
| Mean number of estrous females per day | 2.42 | 1.00–1.40 | 1.40–1.73 |
| Correlation coefficient between male dominance rank and mating | 0.700 | – | – |
| Correlation coefficient between male dominance rank and paternity | 0.587 | – | – |
| Percentage (ratio) of the offspring that an alpha male sired | 22.2 (2/9) | 0 (0/5) | 0 (0/4) |
| References | (5) | (6) | (6) |

(1) Inoue et al. (1990, 1991, 1993); (2) Soltis et al. (1997a,b, 1999); (3) Takahata (1980, 1982a,b, 1999); (4) Inoue and Takenaka (2007); (5) Soltis et al. (2001); (6) Hayakawa (2008)

[a] The males that were observed to copulate with females

[b] The number of adult group males/the number of adult females

[c] Result from a year (1988)

The second factor affecting the reproductive success of dominant males is the number of rival males. Males compete with not only members of the same group but also non-group males to gain mating chances with females. During the mating season, the number of non-group males visiting a heterosexual group positively correlates with the number of estrous females in the group (Takahashi 2001; Hayakawa 2007). As the number of visiting non-group males increases, displays by both alpha and non-group males escalate, and group males cooperatively defend receptive females against non-group males (Yamagiwa 1985). Females, on the other hand, often seek an opportunity to copulate with such non-group males on the periphery of and outside a group (Takahashi 2001; Hayakawa 2007) (Fig. 10.2). At Yakushima, where intergroup encounters provide mating chances between females and males from different groups, the frequency of aggressive behaviors during encounters was significantly higher during the mating season than during the nonmating season. This observation indicates that group males guard females from the males of different groups (Saito et al. 1998). However, when such guarding of females by group males is unsuccessful, non-group males could sire offspring. Hayakawa (2008) reported that the group alpha male had not sired offspring despite the presence of only a small number (1–2 on average) of estrous females per day. In contrast, non-group males had sired 5 of 9 offspring. This circumstance resulted from a small number of group males and an injury of the alpha male by aggression from the non-group males, which led to ineffective defense of receptive females against visiting non-group males.

**Fig. 10.2** Females often consort with non-group males and engage in mating outside a group (Kinkazan Island)

## 10.3 Mating Strategies in Females

### *10.3.1 Within-Species Variation in Estrous Pattern*

Table 10.2 represents the patterns of female estrus in some local populations with different habitats. At Arashiyama and Yakushima, almost all (>95%) females, those which had no infant under 1 year of age, that is, could potentially conceive in a given mating season, displayed estrous signs, and indeed mated with males. In contrast, at Kinkazan, even when females had no infant under 1 year of age, the ratio of females that expressed estrus differed between years: in 1997, all females (100%) without an infant under 1 year of age mated with males; in 1999, only 45.5% did so. Japanese macaques are seasonal breeders, and females generally have repeated ovarian cycles during the mating season unless they have conceived. The mean number of ovarian/menstrual/estrous cycles per female in the mating season is 2.6 (range, 0–6), 2.4 (range, 1–3), and 2.0 (range, 1–3) for the females at Arashiyama and those in the Yakushima A and M groups, respectively. At Kinkazan, the number of estrous cycles was relatively low, that is, on average 1.4 (range, 1–3) in 1997 and 0.5 (range, 0–1) in 1999. In addition, all females with repeated ovarian cycles in 1997 were young (≤6 years) or old (≥17 years), although such females sometimes do not show a normal cycle (Takahata 1980; Nozaki et al. 1995), whereas other females conceived during the first cycle.

In Old World monkeys, the relatively prolonged estrous period, and mating even after conception, are common (Dixson 1998). Although postconception mating has been regularly observed both in captivity and in the wild (Enomoto et al. 1979; Nigi and Hayama 1990; Mitsunaga et al. 1992, 1994; Inoue et al. 1993; Soltis 1999), the expression rate of this behavior varies. At Arashiyama, 76.9% of pregnant females showed postconception mating. At Yakushima, the ratio of females showing postconception mating was different between adjacent groups in the same year, that is, it was 100% in the A group and 25.0% in the M group. At Kinkazan, females rarely displayed postconception mating (18.2% in 1997 and 0% in 1999) (see Table 10.2). Moreover, even when females showed postconception mating at Kinkazan, the duration was only 1 day in all cases.

Food environments, which vary between habitats, are considered to affect ovarian activity via nutritional conditions. At Arashiyama, where the macaques are fed artificially throughout the year, the ratio of females who copulated with males during the mating season is higher, and females have a relatively long duration of estrus during the mating season. In addition, Arashiyama females show higher reproductive performance, including higher birth rate, shorter interbirth interval, and younger age at first birth, than the unprovisioned females at Yakushima and Kinkazan (Takahata et al. 1998). The effect of nutrition on ovarian activity was observed in the other provisioned populations as well: severe reduction in artificial feeding caused a decrease in the birth rate (from 57% to 26%) and a delay in the age at first birth (from 6 to 9 years) at Koshima (Watanabe et al. 1992).

Not only artificial feeding but also food availability in the natural habitat could influence ovarian activity. Females at Kinkazan rarely exhibit postconception mating and have a shorter total duration of estrus than those in other populations (see Table 10.2). In the warm-temperate evergreen forest at Yakushima, high-quality foods such as fruits and seeds are available throughout the year, whereas in the cool-temperate deciduous/coniferous forest at Kinkazan, high-quality foods are available only in limited seasons (Agetsuma and Nakagawa 1998). Therefore, it is expected that ovarian activity is more severely constrained by the ecological conditions at Kinkazan. In a cool-temperate zone among the habitats of Japanese macaques, considering that the macaques need to accumulate body fat before the winter comes, that is, during the mating season (Nakagawa 1989; Nakayama et al. 1999; see also Chap. 5), females may be less able to expend time and energy on mating.

At Kinkazan, the availability of nuts, the main food during the mating season, strongly affects the onset of estrus (Takahashi 2002). The nut crops were poorer in 1999 than those in 1997 (Tsuji et al. 2006), and thus, in 1999, not all females without infants might come into estrus, and females displaying estrous signs did not repeat the ovarian cycle even when they failed to conceive during the first cycle (see Table 10.2). In addition, the first ovulation of each female occurred later in 1999 (between November 11 and November 23) as compared to 1997 (between October 18 and November 6) (Fujita et al. 2004). As Japanese macaques are seasonal breeders, they may have an optimal endpoint of the mating season, and for reasons of both late start of ovarian cycle and poor nutritional conditions, the females might have waited for a chance to breed in the next year rather than continue the effort with an unlikely prospect of conception in 1999.

In addition to the ecological factors, social factors mediate female estrous patterns as well. At Yakushima, females showed different estrous patterns between two adjacent groups: the total estrous duration was much longer in the M group than that in the A group (see Table 10.2). In the M group, at the beginning of the mating season, multiple females came into estrus simultaneously by coincidence (up to seven females were in estrus in one day). Because only two adult males were available in the M group, females gained non-group males as additional mating partners. Group males could not prevent all the estrous females from mating with non-group males, and the mating attempts by non-group males eventually caused group takeovers in succession. Okayasu (2001) suggests that females in the M group prolonged estrus to increase the number of potential mates by attracting males from outside the group. By contrast, females in the A group, where fewer females were in estrus simultaneously, had less chance to mate with non-group males because group males cooperatively chase away non-group males. In addition, females in the M group may develop excessive sexuality because of the constant presence of unfamiliar non-group males and the frequent takeovers (i.e., social context-dependent estrus) (Okayasu 2001). However, the physiological mechanism by which these social factors facilitate ovarian activity remains unclear.

**Table 10.2** Reproductive features in the Arashiyama, Yakushima, and Kinkazan populations

| Group<br>Year | References | Duration of menstrual (m)/estrous (e)/ovarian (o) cycles<br>Mean ± SD<br>Range<br>*n* (cycles) | Number of menstrual (m)/estrous (e)/ovarian (o) cycles in the mating season<br>Mean ± SD<br>Range<br>*n* (females) | Total duration of estrus<br>Mean ± SD<br>Range<br>*n* (females) |
|---|---|---|---|---|
| Arashiyama B[a] | (1) | 26.5 ± 9.1 (m) | 2.6 ± 1.5 (m) | 35.0 ± 26.4 |
| 1976 | | 8–52 | 0–6 | 0–116 |
| | | 73 | 87 | 87 |
| Yakushima A[b,d] | (2) | 26.2 ± 1.3 (e) | 2.4 ± 0.7 (e) | 12.6 ± 4.1 |
| 1984 | | 16–35 | 1–3 | 1–40 |
| | | 15 | 11 | 11 |
| Yakushima M[b,d] | (2) | – | 2.0 ± 0.9 (e) | 55.6 ± 6.0 |
| 1984 | | – | 1–3 | 22–71 |
| | | – | 8 | 8 |
| Kinkazan A[c,d] | (3) | 35 (o) | 1.4 ± 0.6 (o) | 19.0 ± 6.5 |
| 1997 | | 35 | 1–3 | 9–34 |
| | | 1 | 14 | 14 |
| Kinkazan A[c,d] | (3) | – | 0.5 ± 0.5 | 3.3 ± 4.7 |
| 1999 | | – | 0–1 | 0–12 |
| | | – | 11 | 11 |

| Group<br>Year | References | Ratio of females who copulated with males<br>Ratio<br>*n* (females) | Birth ratio in the following birth season<br>Ratio<br>*n* (females) | Ratio of females who conceived in the first estrous cycle<br>Ratio<br>*n* (females) | Ratio of females who showed postconception<br>Ratio<br>*n* (females) |
|---|---|---|---|---|---|
| Arashiyama B[a] | (1) | 0.954 | 0.598 | 0.750 | 0.769 |
| 1976 | | 87 | 87 | 52[e] | 52[e] |
| Yakushima A[b,d] | (2) | 1.000 | 0.364 | 0.000 | 0.250 |
| 1984 | | 11 | 11 | 4[e] | 4[e] |
| Yakushima M[b,d] | (2) | 1.000 | 0.375 | 1.000 | 1.000 |
| 1984 | | 8 | 8 | 3[e] | 3[e] |
| Kinkazan A[c,d] | (3) | 1.000 | 0.786 | 0.909 | 0.182 |
| 1997 | | 14 | 14 | 11[e] | 11[e] |
| Kinkazan A[c,d] | (3) | 0.455 | 0.091 | 1.000 | 0.000 |
| 1999 | | 11 | 11 | 1[e] | 1[e] |

(1) Takahata (1980); (2) Okayasu (2001); (3) Fujita et al. (2004, unpub. data)

The subjects are the females aged [a] 3 or more years; [b] 4 or more years; [c] 6 or more years

[d] The subjects are the females who had an infant under 1 year of age and did not show any estrous sign, which were excluded because the wild females rarely give birth in the consecutive years.

[e] The females that had conceived in the mating season

### 10.3.2 Concealment or Advertisement of the Timing of Ovulation

Females of many primate species, in contrast to most mammals, show prolonged sexual receptivity beyond their fertile periods, which is limited to a few days at most (Dixson 1998). Female Japanese macaques in the enclosed group began mating 5 weeks before ovulation and continued for up to 10 weeks after ovulation (Soltis et al. 1999). As already described, postconception mating, which never leads to reproduction, is also common in many populations of Japanese macaques (Takahata 1980; Mitsunaga et al. 1992; Soltis et al. 1999; Okayasu 2001). Accordingly, the reasons why females have considerably longer receptivity despite the potential costs and risks of mating have been discussed for a long time.

Several hypotheses about the compensatory benefit of extended sexual receptivity have been proposed. The most common one is concealing of the timing of ovulation from males, which prevents dominant males from monopolizing access to fertile females and enables females to exhibit mate-choice behaviors toward males of various ranks (Sillén-Tullberg and Møller 1993). In addition, concealing the timing of ovulation facilitates mating with multiple males, which includes potential benefits such as gain in paternal investment from more than one male (Small 1990), improved defense by increasing the number of males per group (van Schaik et al. 2000), or inhibition of infanticide through confusing paternity (Hrdy 1979).

Although females may conceal the timing of ovulation through a considerably longer duration of receptivity, they have developed signals to indicate the timing of ovulation. For example, in some species of Old World monkeys and apes, females show sexual swelling that reaches maximum size in the periovulatory period (Zinner et al. 2004). In Japanese macaques, although sexual swelling is rarely observed in fully mature females (Enomoto 1974, 1975; Mori et al. 1997), reddening of the facial and perineal skin gradually increases during the follicular phase, and reaches a peak in the periovulatory period (Fujita et al. 2004) (see Fig. 10.3). In addition, cervical mucus with a specific smell, which is thought to function as a sex pheromone (Dixson 1998), also increases in volume during estrus (Enomoto 1974; Nigi 1975). In addition to these physical attractions, behavioral sexual activities such as solicitation for mating, vocalization, and proximity maintenance with males also increase during estrus (Enomoto et al. 1979).

These visual, olfactory, and behavioral traits change with the ovarian cycle, and are controlled by sex hormones, especially estrogen (Dixson 1998), and males may recognize the timing of ovulation using these cues. In the "graded-signal hypothesis," which was originally proposed to explain the evolution of exaggerated swelling (Nunn 1999), Japanese macaque females would indicate their fertile phase in a probabilistic manner. This mechanism allows dominant males to guard mating partners during the time of high probability of ovulation, and, on the other hand, subordinate males to mate during times of low (nonzero) probability of ovulation. Therefore, it is thought that females not only receive infant protection from dominant males through increased paternity certainty but also reduce the risk of infanticide because other males are also the possible fathers of the offspring. Under the graded-signal

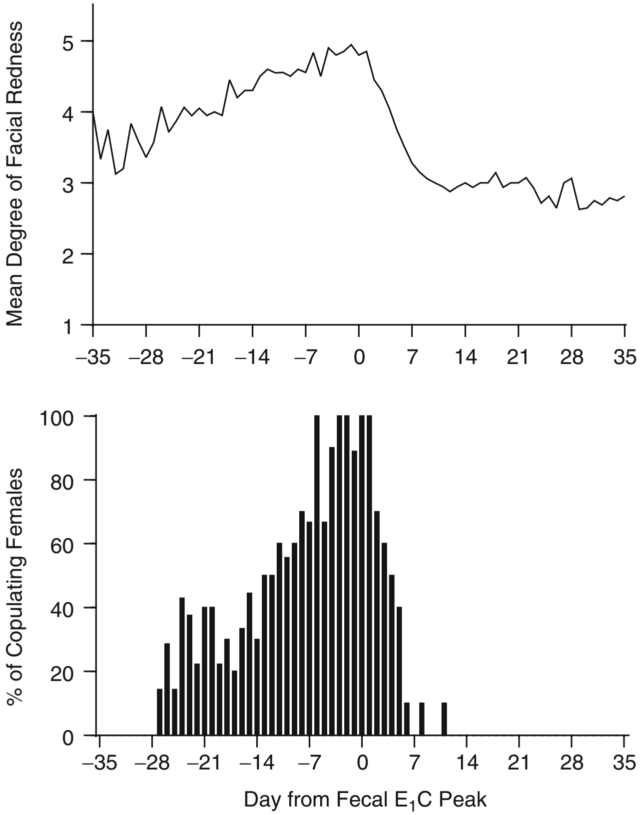

**Fig. 10.3** Changes in facial redness ('1' to '5', *y*-axis, represents minimum to maximum) and percentage of the females that copulated with males during the ovarian cycle in ten female cycles on Kinkazan Island. Day 0 represents the ovulation time that is inferred from the fecal hormonal ($E_1C$) profiles. (Redrawn from Fujita et al. 2004 with permission of John Wiley & Sons, Inc.)

hypothesis, the longer duration of receptivity associated with exaggerated swelling is the important factor in how exaggerated swellings can solve the female dilemma. In the case that two or more females are simultaneously receptive through longer duration of receptivity, the optimal strategy for a dominant male is to guard only a female of maximum swelling, which is more likely to ovulate. On the other hand, because ovulation is signaled only approximately, error in ovulation time is required for a male to guard a female for a longer period to exclude other males from paternity. However, longer duration of female receptivity makes it less likely that a male will completely monopolize a female during her entire window of fertility, which enables her to mate with additional males. However, according to the graded-signal hypothesis, females of seasonal breeders are more likely to overlap in their receptivity simply by chance, and so mechanisms to increase overlap, as achieved through exaggerated swelling, are not needed. Indeed, exaggerated swelling is found more in non-seasonally breeding species (Nunn 1999). Female Japanese macaques, which are strictly seasonal breeders, have no exaggerated swelling but have other physical traits such as redness of sexual skin that also indicate their fertile phase approximately (Fujita et al. 2004) (see Fig. 10.3). Because ovulation time, even in the seasonal breeders, is considerably distributed in several months and rarely overlaps (Fujita et al. 2004), it may be advantageous for females to signal their fertility approximately (i.e., not exactly) to avoid monopolization by a male and exert female mate choice effectively.

Although many hypotheses about the female strategy of concealing or advertising the timing of ovulation have been proposed, there is little empirical evidence indicating to what extent males can indeed distinguish the fertile phase of females. In the study of long-tailed macaques, it was reported that interest in females by males was strongest during and around the fertile phase, indicating that males were able to recognize the fertile phase at least to some degree. In addition, the interest of males in females positively correlated with female estrogen levels, suggesting that males use estrogen-related cues (Engelhardt et al. 2004). In Japanese macaques, many studies conducted both in captivity and in the wild found evidence that mating is most concentrated during the fertile phase (Enomoto et al. 1979; Inoue et al. 1991; Mitsunaga et al. 1992, 1994; Soltis et al. 1999; Fujita et al. 2004) (see Fig. 10.3), which may be the result of the ability of the males to recognize the reproductive status of females. However, several studies revealed that dominant males did not always succeed in mating during the fertile phase (Inoue et al. 1993; Fujita et al., in preparation) nor did they sire offspring (Inoue et al. 1993; Hayakawa 2008; Inoue and Takenaka 2007), which suggests that males have a relatively low degree of accuracy in pinpointing the time of ovulation.

### 10.3.3 Female Mate Choice

Female Japanese macaques are observed to selectively choose particular males as mates: although they attempt to maintain proximity with males or actively solicit males for mating (Enomoto 1974, 1975, 1978; Enomoto et al. 1979; Takahata 1980; Huffman 1987; Soltis et al. 1997a,b), they reject mounting attempts by unfavorable males (Yamagiwa 1985; Huffman 1987, 1991b, 1992). In adaptive models, mate choice can evolve when males bring females either direct (material) or indirect (genetic) fitness benefits. Female primates sometimes choose large, powerful, or dominant males when these males provide access to food, paternal care, or protection from other infanticidal males (Paul 2002). However, in many studies on Japanese macaques, higher-ranking males did not always achieve better mating success (Takahata 1980; Huffman 1987, 1991b, 1992; Perloe 1992; Soltis et al. 1999) (see Table 10.1). Detailed behavioral observation for the captive group revealed that females did not choose males on the basis of rank, age, or body weight. On the other hand, male display behavior was the only trait that correlated with male proceptive behaviors (Soltis et al. 1999). Although the benefit of choosing males with the most frequent display behavior is unclear, a likely explanation is that this conspicuous behavior may exert an influence on female choice by signaling the location of potential mates.

Female Japanese macaques sometimes choose novel males with shorter breeding tenure (Takahata 1982a,b; Huffman 1987, 1991a,b, 1992), as reported for other macaques (Manson 1995; Bercovitch 1997). Moreover, in the provisioned group, some male and female pairs, maintaining long-term affiliative relationships, known as "peculiar proximate relation (PPR)," were observed to avoid mating with each other (Takahata 1982a). Paternity analysis in the Arashiyama E group revealed that male shortness of tenure rather than dominance or seniority was associated with reproductive success (Inoue and Takenaka 2007). These novel males often include relatively young and lower-ranking males, because male rank tends to increase with his tenure (Suzuki et al. 1998). However, at Yakushima, where the takeover of a group by a fully mature non-group male often occurs (Suzuki et al. 1998), this new alpha male enjoys high mating success (Hayakawa 2007). A most plausible explanation is that mating with novel males maintains the genetic diversity of the offspring to which a female gives birth during her lifetime (Wolfe 1986). Another explanation is that, as Japanese macaques are matrilineal, that is, sexually mature males transfer between groups, female mate choice for novel males could promote such male transfers (Takahata et al. 1999) and facilitate male recruitment for the purposes of group defense (Wrangham 1980).

In the wild populations, mating with non-group males, which are novel to females, often occurred, accounting for 41% (186/452) and 50% (62/125) of observed matings with ejaculation at Yakushima (Sprague 1991) and Kinkazan (Takahashi 2001), respectively. Such mating often occurred on the periphery of or outside the group (Takahashi 2001; Hayakawa 2007) and led to successful siring (Hayakawa 2008). At Kinkazan, during the periovulatory period, 39 (75%) of 52 observed matings in six females (7 cycles) were with non-group males, 13 (25%) matings were with the group beta male with short tenure (≤2 years), and 0% (0/52) were with the alpha group male with long tenure (≥5 years) (Fujita et al., in preparation). Mating with non-group males sometimes results in social events. At Yakushima, mate choice for non-group males by females and the shortage of group males possibly caused group fission (Yamagiwa 1985).

### *10.3.4 Promiscuous Mating*

One hypothesis states that females follow a strategy of mating with multiple males rather than choose particular males as mating partners, although the two patterns are not mutually exclusive (Soltis 2004). In fact, female Japanese macaques have been observed to mate with multiple males (up to four) even in a single day (Matsubara and Sprague 2004). According to the sexual selection hypothesis, males increase reproductive opportunities by killing unrelated and unweaned offspring (i.e., infanticide), thus hastening the mother's next ovulation (Hrdy 1979). In such situations, females should develop counter-strategies to confuse paternity by mating with multiple males. In Japanese macaques, although infanticide is not common, there are a few reports that male aggression toward the infants resulted in killing them (Yamada and Nakamichi 2006; Izawa 2009). In cases that have been reported in Japanese macaques, infanticide was likely to occur under three conditions: (1) in the pre- or early mating season, (2) a threatening male is least likely to be the father of the infant, and (3) there are no resident males to defend the infant against attacks (Yamada and Nakamichi 2006). Moreover, there is a report that at Yakushima, where infanticide by non-group males had been observed, males attacked infants of non-mates during the last mating season eight times more often than those of former mates (Soltis et al. 2000). This observation suggests that female mating with multiple males can inhibit male-to-infant contact aggression, even in this species.

As a second explanation for promiscuous mating, when females are unlikely to experience infanticide, mating with multiple males is a consequence of sexual harassment (Wolff and Macdonald 2004). During the mating season, male aggression toward the females increases (Enomoto 1981; Soltis et al. 1997b, 1999; Barrett et al. 2002). In addition, male aggression positively correlates with increased mating (Enomoto 1981; Barrett et al. 2002) and with female initiation and maintenance of proximity with the aggressor male (Soltis et al. 1997b; Soltis 1999). This evidence indicates that males use force to coerce females to mate. Accordingly, females may receive mating by unfavorable males to avoid further aggression. In fact, female Japanese macaques tend to copulate with higher-ranking males with a long tenure, which are unfavorable to females (as already described), only when fertilization is unlikely or impossible (Inoue and Takenaka 2007; Fujita et al., in preparation). This finding suggests that females accept the attempt of mating by these males to avoid sexual harassment.

## 10.4 Conclusions and Future Research

Japanese macaques have various mating strategies through inter-and intrasex competition. Males compete for access to receptive females, and hence, dominant males have the priority of access, whereas subordinate males can copulate by sneaking. Male also compete via sperm competition when mating with multiple males occurs during the fertile period. On the other hand, females choose mating partners by rejecting mating attempts by unfavorable males and by soliciting mating from the favorable males. In addition, females mate with multiple males during the mating period, which may both prevent infanticide by males that have sired no infant and facilitate sperm competition.

One point that remains unclear is whether the females change mating strategies during the ovarian cycle. This possibility is suggested by observations that females change mating partners between conditions when conception is likely to occur and when it is not (Matsubara and Sprague 2004; Inoue and Takenaka 2007; Fujita et al., in preparation). Moreover, the extent to which males can distinguish the female fertile phase, which can influence the efficiency of male guarding of females, is still unclear. The current techniques of hormonal assay using noninvasive samples, such as urine and feces, to monitor ovarian cycle may be useful for addressing these problems; this is because this technique can be applied even to wild animals, and hence, the correlation of behavioral observation in the natural setting and the hormonal profile can be tested.

The interaction of male and female mating strategies in Japanese macaques is summarized in Fig. 10.4. The OSR determines the ability of the dominant males to monopolize all the receptive females. When only a few receptive females are present (low OSR), as the priority access model predicts, dominant males can monopolize females and have higher reproductive success. In contrast, when a larger number of females simultaneously come into estrus (high OSR), monopolization by dominant males is not likely to occur and the female's mating strategies such as mate choice or multiple mating can prevail.

The OSR is affected by several factors. Female reproductive status and ovarian activity are strongly affected by ecological conditions via the nutritional condition. In the wild unprovisioned populations, females give birth on an average of every 2

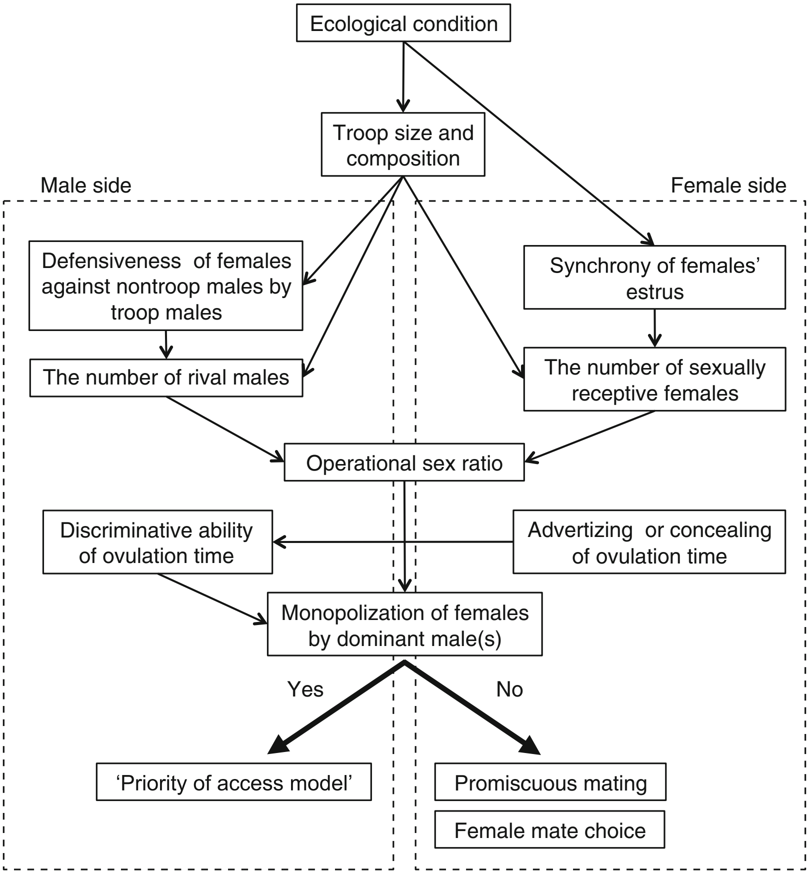

**Fig. 10.4** Interaction of male and female mating strategies and its affecting factors

years (Takahata et al. 1998), and thus the number of sexually receptive females fluctuates with the year. In addition, the total duration of estrus per female during the mating season, which depends on the duration of estrus per ovarian cycle, the number of ovarian cycles, and the occurrence of postconception mating, differ between populations (see Table 10.2). Longer estrous duration during the mating season necessarily causes estrous synchrony, resulting in more estrous females per day. On the other hand, the number of males comprising the OSR can also change according to the condition. The number of non-group males visiting a group also differs between years, depending on the number of estrous females in a group (Takahashi 2001, 2004). In addition, when only a few males are present in a group, defense of females against non-group males by group males does not work effectively, and non-group males gain more chance of mating with females (Yamagiwa 1985; Okayasu 2001; Hayakawa 2007).

Because of these factors, the OSR can differ among populations in different habitats and fluctuate from year to year in a single group. Therefore, whether the male or female mating strategy prevails depends on the situation. As a result, there is a variation in the association between male dominance rank and mating/reproductive success (see Table 10.1). Japanese macaques are widely distributed in various habitats and have various social organizations (Yamagiwa and Hill 1998), and more data are needed to clarify the variation in mating strategies among different habitats.

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# Chapter 11: Lifetime Social Development in Female Japanese Macaques

**Masayuki Nakamichi and Kazunori Yamada**

## 11.1 Introduction

In the majority of primate species, the infant is born with grasping extremities of all four limbs, allowing it to continue clinging to its mother's fur without support. Therefore, regardless of the mother's activity patterns, the infant is very likely to spend most of its time in contact with her in the early stages of development. In tandem with the development of locomotor abilities, the infant gradually increases the time spent away from her, thus extending its social milieu. Even after the infant is weaned from its mother, it still maintains a relationship with the mother throughout its immature days. These developmental changes in the mother–offspring relationship in the infant's immature days are universal among almost all primate species, including Japanese macaques (*Macaca fuscata*); behavioral differences between male and female infants, meanwhile, gradually increase with increasing age.

While most male Japanese macaques leave their natal groups upon maturity (Nishida 1966; Kato 2001), female Japanese macaques usually remain in their natal groups throughout their lives. Therefore, throughout their lives – which can be as long as 20 years or more (Itoigawa et al. 1992) – female Japanese macaques develop and maintain close, long-term relationships not only with females closely related to them through maternal lines but also with some unrelated females in the group (Nakamichi and Yamada 2007).

Among Japanese macaque populations inhabiting a variety of habitats, some intraspecific variations could be expected with respect to how females interact with group members, including their own offspring, throughout their lifetime development. For example, Johnson and Southwick (1984) reported that mother–infant

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relationships in rhesus macaques (*Macaca mulatta*) did not differ across three different habitats in Nepal and India, whereas in savanna monkeys (*Cercopithecus aethiops*), the rate at which mothers rejected their infants differed between two habitats in Kenya, leading to a difference in interbirth intervals (Hauser and Fairbanks 1988). Unfortunately, few studies have directly focused on variations in behavioral responses to ecological conditions with respect to both infant social development and behavioral changes in adult females with increasing age in Japanese macaques.

The present chapter, therefore, focuses on describing lifetime social development of female Japanese macaques with respect to developmental stages such as infant (<1 year old), juvenile (between 1 year and the first estrus at around 3.5 years), adolescent (from the first estrus to the first birth at around 5–7 years), and adult (from the first birth to death), on the basis of behavioral studies conducted in several provisioned or wild groups (Fig. 11.1). Whenever possible, we address intraspecific variations in certain limited stages of development or some aspects of the females' social relationships.

## 11.2 Infants and Juveniles

### *11.2.1 Foraging*

Although Japanese macaque mothers continue to nurse their infants at least during the first year (Tanaka 1992), infant Japanese macaques begin to lick or chew solid objects (edible or inedible) such as stones, small clods, and twigs from as early as 2 weeks of age; they eat edible solid objects at 5 weeks of age (Hiraiwa 1981; Ueno 2005). They also begin to use the cheek pouches to store food temporarily from 8 to 10 weeks of age onward (Hasegawa and Hiraiwa 1980; Hiraiwa 1981). Few individual differences appear in the timing of each behavior related to solid food intake (Hiraiwa 1981).

Hasegawa and Hiraiwa (1980), who observed a provisioned group of Japanese macaques in Boso Peninsula, Chiba Prefecture, were the first to describe qualitatively the possibility that infants acquire the food repertoire from their mothers and other group members, on the basis of observations that an infant tried to eat the same object that its mother was eating and often nuzzled foraging macaques. The findings of Ueno (2005), who observed infants and 1-year-old juveniles longitudinally in a provisioned group in Arashiyama, Kyoto Prefecture, successfully exemplify the presence of the tendency toward synchronous feeding in infant and 1-year-old juvenile Japanese macaques: young macaques were very likely to not only show feeding behavior when their closest neighbors were feeding within 1 m of them much more frequently than when their neighbors were not, but also feed on the same food item. In particular, the tendency for infants to feed on the same items as their neighbors did became more apparent with increasing age, during the first 6 months after birth, and this tendency was maintained in 1-year-old juveniles. Such neighbors were mothers and peers. Tarnaud and Yamagiwa (2008), who

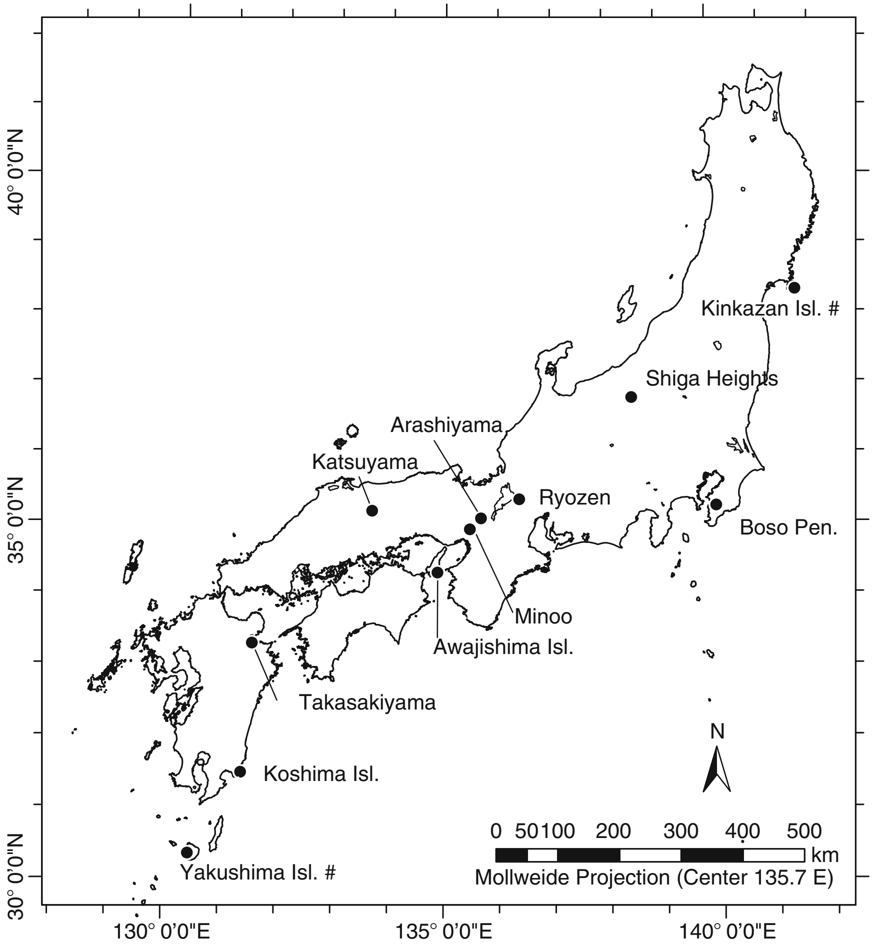

**Fig. 11.1** Japanese macaque study sites discussed in the present chapter. Site names marked with "#" indicate wild groups; those without "#" are provisioned groups. (The base map is originated from "Boundary data of cities, towns and villages of Japan ver. 6.2" by ESRI Japan Corporation, with permission)

observed wild groups of Japanese macaques on Yakushima Island, Kagoshima Prefecture, also found that intensive observations, defined as the act of turning the head toward the foraged food and/or location of a foraging individual, were directed by infants aged between 7 and 12 months and juveniles aged between 1.5 and 2 years toward elders engaging in plant and invertebrate foraging; additionally, such observations were more frequent in infants than in juveniles, and the vast majority of intensive observations were directed toward the mother. While it is apparent that mothers directly contribute to the survival of their infants through nursing, the findings by Ueno (2005) and Tarnaud and Yamagiwa (2008) show that mothers also provide the opportunity for their infants to acquire the repertoire of edible food items by permitting their infants to co-feed with them, which could lead to the social transmission of food-selection habits.

Close attention paid by young macaques toward their mothers or other elders is needed to acquire not only a large dietary repertoire but also the food-processing method. Although most adult macaques of both sexes within a provisioned group at Katsuyama, Okayama Prefecture, simply scraped dirt from grass roots with their hands as soon as they pulled the grass from the soil, and then ate it, some adult females carried grass roots to the river, where they washed the roots and then ate them (Nakamichi et al. 1998). They usually pulled one root at a time and set it aside to form a pile consisting of several roots, and they then carried the entire pile of roots to the river to wash and eat. The individuals who were seen performing this carrying and washing behavior consisted of several mothers and their adult daughters, all of whom belonged to high- and middle-ranking kin-groups. No adult males were recorded as carrying and washing grass roots. As immature macaques were rarely recorded as having dug roots as long as 10–20 cm, such tasks may be difficult for them; however, they were sometimes seen watching their mothers washing and eating the roots while sitting nearby and would pick up a half-eaten root to eat (Nakamichi et al. 1998). It is probable that young adult females who watched their mothers carry and wash grass roots when they were young begin to perform such behavior after they mature enough to pull grass roots out without any difficulty. In other words, the behavior of carrying and washing grass roots is likely to be transmitted from mothers to their daughters, and this tendency might be highly related to the fact that juvenile females spend much more time with their mothers than do juvenile males (Nakamichi 1989; see also Sect. 11.2.3).

Acquisition by the young of new behavioral patterns other than the aforementioned food-related behaviors, acquired by paying close attention to or intensively observing their elders, has also been reported with regard to louse egg-handling techniques during social grooming (Tanaka 1995, 1998; see also Chap. 9).

### 11.2.2 Infant Carriage by Mother

As does nursing, infant carriage by the mother contributes directly to infant survival, because infants, particularly those under 6 months of age, do not always manage to follow the group members as they venture uphill and downhill into the forest, even though they develop locomotor abilities rapidly during the first few months after birth. According to Hiraiwa (1981), infants at 4 weeks of age begin to cling to the backs of their mothers, although there is a wide variation in this onset. Moreover, when the group was in progression, even 12-month-olds were carried dorsally on 40% of observed occasions.

Yamada and Nakamichi (under review) reported developmental changes in ventral and dorsal carriage by the mother and in the infant's following of its mother in the Katsuyama group. While ventral carriage was most frequently used in the first 4 months after birth, in the next 4-month period (i.e., 5–8 months of age), the occurrences of ventral carriage decreased drastically and those of dorsal carriage increased. In the third 4-month period, following by the infant occurred much more frequently than dorsal carriage; in the fourth 4-month period, the infant's following was still frequently observed, but dorsal carriage was rarely observed and no ventral carriage was observed near the feeding site. In the Katsuyama group, moreover, almost all infants around 12 months of age were found to be carried dorsally at least once a day while they remained near the feeding site, although mothers rarely carried their infants for long distances (Nakamichi, unpublished data). Moreover, some mothers in the Katsuyama group were recorded as carrying juveniles as old as 2 years dorsally, albeit infrequently (Nakamichi, unpublished data). Almost all infants around 12 months of age in the Arashiyama group were also found to be carried dorsally by their mothers (Sukino, personal communication); this was also the case in a provisioned group at Awajishima Island, Hyogo Prefecture (Yamada, unpublished data). More interestingly, some mothers in the Katsuyama group were recorded as carrying one infant ventrally while simultaneously carrying a 1-year-old offspring dorsally (Nakamichi et al. 2004); this was also seen in the Awajishima group (Nakamichi, unpublished data).

In combining these findings from the four provisioned groups, it is a general rule that although infant Japanese macaques around 12 months of age or older are old enough to move by themselves along with group members in mountainous areas, they still seek to ride on the backs of the mothers, albeit infrequently; this tendency indicates that infant Japanese macaques are very likely to be psychologically dependent on their mothers, even after acquiring independence from their mothers in terms of locomotor ability (Nakamichi and Yamada 2009). In other words, clinging to the mother's back allows them to satisfy psychological needs during stressful moments. In fact, when infants and young juveniles show "temper tantrum" behaviors, such as pressing the body to the ground and crying out toward their mothers nearby, they usually stop crying as soon as they are permitted to cling to their mothers' backs.

### *11.2.3 Relationships Between Immature Offspring and Their Mothers*

Some studies of Japanese macaques have examined certain factors that can influence the process by which infants become independent of their mothers with increasing age, including the infant's sex, mother's dominance, and mother's parity. These are well-known traditional factors (Berman 1984); here, we focus on the first two factors, while the third is examined later from the point of view of adult females (i.e., mothers) (see Sect. 11.4.1).

Itoigawa (1973) found that, in the Katsuyama group, female infants spent more time in contact with their mothers' ventral surface than male infants and were restrained and retrieved more frequently than male infants throughout the first

8 months of life. On the other hand, Suzuki et al. (1984), in studying the Arashiyama group, found no consistent differences in mother–infant contact between female and male infants during the first 6 months of life. Tanaka (1989) points out that an infant's sex rarely has a great influence on mother–infant interactions during the first 8 months, as seen in a provisioned group at Shiga Heights, Nagano Prefecture. Nakamichi (1989), who observed all infants of a birth cohort during the first 4 years of life in the Awajishima group, reports that the tendency for female infants to stay close to their mothers more frequently than male infants becomes apparent from the second half of the first year onward. Although male juveniles steadily decreased the time spent near their mothers throughout the first 4 years of life, female juveniles did not show such a decrease after the third year of life; instead, they maintained relatively frequent proximity to their mothers (Nakamichi 1989). Koyama (1991) also notes that at Arashiyama, female juveniles between 2 and 4 years of age groomed their mothers much more frequently than did male juveniles, while mothers groomed their daughters as often as their sons. These findings indicate that the difference in life-course between males who leave the natal group and females who remain in it become apparent in the early juvenile days in terms of their relationship with their mothers.

Some studies conducted on captive groups of macaques have shown that infants of low-ranking rhesus macaque mothers tend to spend more time in contact with and being restrained from their mothers more frequently than those of high-ranking mothers (White and Hinde 1975; Tartabini et al. 1980). However, clear differences in mother–infant interactions that accompany intimate physical contact, in terms of the mother's dominance rank, have not been reported in provisioned, free-ranging groups of Japanese macaques (Suzuki et al. 1984; Tanaka 1989). These findings from different free-ranging but provisioned groups of Japanese macaques indicate that infant sex and the mother's dominance rank might have much less influence on mother–infant interactions – at least under 1 year of age – than previously thought.

On the other hand, in provisioned situations where agonistic interactions occur relatively frequently among animals, often because of a scattering of highly preferred foods such as wheat and soybeans within a limited area or timeframe, immature females of high-ranking kin-groups more frequently remained with their mothers in the same feeding blocks to pick up wheat than those of middle- or low-ranking kin-groups, and this was also true for immature males (Imakawa 1988). These findings indicate that the higher a mother's dominance rank, the more effectively she serves as a secure "base" for her immature offspring of either sex, at least during feeding times (Imakawa 1988).

### *11.2.4 Relationships of Immature Females with Group Members Other than Mothers*

Initially, infant Japanese macaques are completely dependent on their mothers; however, they rapidly increase the amount of time they spend away from their mothers and thus extend their physical and social environments (Itoigawa 1973;

Hiraiwa 1981; Suzuki et al. 1984). Because the birth season of Japanese macaques is limited to a few months from spring to summer (Ando and Ukai 1983; Fooden and Aimi 2003), individual differences in the development of motor skills among infants of the same cohort are rarely apparent. As a result, infants usually begin to extend interactions with each other from around the second month of life onward (Suzuki et al. 1984); throughout the first year of life, they also spend much more time with same-aged infants than with older individuals other than their mothers (Nakamichi 1989). On the basis of social interactions, including social play, among infants in the Arashiyama group, Norikoshi (1974) found that the ranks of infants as young as 12 weeks of age were parallel to those of their mothers. Suzuki et al. (1984) confirm that there is a similar but clearer tendency among infants at the age of 6 months within the same group.

In the Awajishima group, juvenile females aged 2–4 years maintained roughly equal proximity to female group members of various age differences from their own (i.e., immature to adult females) and to infants of both sexes; juvenile males, meanwhile, maintained frequent proximity to males of the same and similar ages (Nakamichi 1989). Moreover, juveniles of both sexes in the Awajishima group showed a consistent preference for proximity within their cohort to certain same sex individuals whose dominance ranks were immediately adjacent to their own throughout the first 4 years of life; such proximity-based relationships between peers of the same sex largely reflected those between their mothers (Nakamichi 1996).

The characteristics for social relationships of immature macaques in the Awajishima group, which were depicted by proximity data, have been witnessed in some other groups of Japanese macaques through actual interactions such as play. At both Arashiyama (Koyama 1985) and Katsuyama (Imakawa 1990; Koyama 1998), females tended to play with individuals of the same age and same sex before the age of 2 years, but thereafter, they tended to play with younger macaques of both sexes; meanwhile, males tended to select individuals of the same age and same sex as play partners in their immature days, with a tendency to decrease frequency of play and decrease the number of play partners with increasing age, regardless of sexes. The tendency for female juveniles to stay near younger individuals, in particular, infants and 1-year-olds of either sex, was also found in a provisioned group in Koshima Islet, Miyazaki Prefecture (Hayaki 1983). Juvenile females in the same group were also reported to have relatively frequent grooming interactions with other juveniles of different ages (Mori 1974).

At Katsuyama, infant-handling, that is, carrying and holding young that are not one's own offspring, was mostly displayed by older juvenile females aged 3 and 4 years (96% of all observed caretaking events); infants under 1 year of age were the most frequent targets of infant-handling (90%) (Imakawa 1993). At Koshima, infant-handling performed by 3- to 5-year-old females accounted for as little as 22% of all caretaking events, while 1-year-old juveniles most frequently (44%) displayed this behavior; 85% of the target animals were infants (Mori 1986). At Boso, 2-year-old females displayed infant-handling most frequently, followed by 3-year-old females and then 1-year-old ones (Hiraiwa 1981). In the captive group at Roma Zoo, juvenile females (aged 1–3 years) and nulliparous adolescent females (aged 4–7 years) displayed infant-handling most frequently (Schino et al. 2003). In contrast, neither adult females with maternal experience nor males showed much interest in the infants of other females. Therefore, the tendency for juvenile females to display infant-handling much more frequently than juvenile males or adult females is common across the different groups, but the age at which female juveniles most frequently display infant-handling differed among the groups.

In summary, across the four provisioned groups of Japanese macaques, juvenile females were inclined to maintain proximity-based relationships with group members who usually formed the center of the group; those females actually tended to interact with younger individuals through social play, grooming, and infant-handling, although still rarely maintaining affiliative relationships with adult females other than their mothers through actual interactions such as grooming. With regard to male juveniles, their inclination to interact with males of the same or similar age was apparent, even before the spatial shifts from the center to the periphery of the group.

These findings from different groups indicate that, without clear intraspecific variations, both female and male juvenile Japanese macaques begin to prepare for their respective adult roles as early as around the second year of life, at which time they are still very likely to maintain frequent proximity to their mothers (Nakamichi 1989). Note that among both female and male juveniles, the process of developing social relationships with other group members could be influenced by the presence or absence of older siblings, because juveniles could acquire more opportunities to interact with elder animals by way of their older siblings (Kojima 1996).

## 11.3 Social Relationships of Adolescent Females with Group Members

The life stage of adolescence is defined as the interval from the onset of puberty to the beginning of effective reproduction (Pereira and Altmann 1985). Therefore, it is difficult to categorize adolescent females with respect to age period, because Japanese macaque females begin to experience first ovulation – one of the internal signs of the onset of puberty – at around 3.5 years of age, but the actual age differs from female to female (Nigi 1982). The same is also true for the age at which females first give birth: it extends from as early as 4 years of age to over 10 years of age, and it greatly depends upon nutritional conditions (Watanabe et al. 1992). Here, whenever possible, we focus on how and with whom nulliparous females aged around 4 years or more socially interacted, compared to females experiencing their first births.

Kudo (1986) classifies adolescent females into three classes in terms of their social interactions with group members: (1) sociable females who have grooming interactions with a relatively larger number of unrelated females, who tend to groom high-ranking females and/or females with an infant or juvenile more frequently than other females; (2) kin-orienting females who concentrate their social interactions on their own close female relatives; and (3) unsociable females who tend to spend little time interacting with group members. Moreover, regardless of typology, each adolescent female had a particular grooming partner who was also an adolescent, but such grooming relationships were likely to disappear after one of the pair gave birth to her first infant. On the basis of these observations at Koshima, Kudo (1986) concludes that the social relationships that each adolescent female formed and maintained with some females might disappear around the time of the first birth, and that new mothers had to reconstruct their social relationships with adult females with offspring. Some primiparous females at Katsuyama were found to interact more frequently with adult females, through affiliative behaviors such as grooming, after giving birth to the first infant, compared to before its birth (Nakamichi, unpublished data). This finding indicates that some young adult females become more social after having their first infant. Grewal (1980) also points out the differences in social interactions between nulliparous and primiparous females aged 4–7 years at Arashiyama.

Yamada et al. (2005) examined the grooming relationships of adolescent females at Katsuyama who had no experience of giving birth and ranged in age from 5 to 7 years, with a special interest in the influence of the loss of the mother on the social development of adolescent females. Although it was expected that the loss of the mother would force orphans to devote less time to grooming interactions than nulliparous adolescent females who still had mothers, orphans without sisters performed grooming interactions as frequently as non-orphans or orphans with sisters; this was because non-orphans maintained grooming interactions with their mothers whereas orphans acquired alternative grooming relationships with other group members. Orphans with sisters developed more grooming relationships with sisters, and orphans without sisters developed grooming interactions with same-aged females and unrelated adult females. Orphans without sisters also had a larger number of grooming partners than did non-orphans. On the basis of these findings, Yamada et al. (2005) concludes that adolescent females have enough social flexibility to develop a grooming network after losing their mothers; in such cases, a lack of close relatives such as mothers and sisters might accelerate socialization among adolescent females.

Mori et al. (1977) report that at Koshima the dominance ranks of nulliparous females were usually lower than those predicted by Kawamura's rules (see Sect. 11.4.3); however, after experiencing the first birth, young adult females tended to acquire the dominance ranks predicted by Kawamura's rules. Because dominance relationships among infants at 12 months of age are parallel to those among their mothers (Koyama 1970; see also Sect. 11.2.4), it is probable that dominance relationsships among same- or similar-aged juvenile females are also parallel to those among their mothers; however, such juvenile females may be still too young to be integrated into dominance relationships among adult females. To stabilize maternal rank inheritance among adult females, it may be necessary for young adult females first to experience a first birth.

The loss of the mother imposes a disadvantage on the daughter, namely, the failure to inherit the mother's dominance rank (Hasegawa and Hiraiwa 1980;

Takahata 1991; Nakamichi et al. 1995a; Kutsukake 2000). On the other hand, the loss of the mother may otherwise benefit orphaned females. Itoigawa (2001) reports that at Katsuyama, two orphaned sisters of a middle-ranking kin-group rose in rank with support from the alpha male, eventually leading to a group fission, in which one group comprising the two orphaned sisters, their relatives, members of other middle- and low-ranking kin-groups, and central high-ranking males became dominant to the other group that comprised females of high-ranking kin groups. In addition, the birth rate of the kin-group of the two orphaned sisters increased. Clearly, adolescent females have great flexibility in the socialization process, allowing some orphaned females to overcome the disadvantage of losing the mother.

## 11.4 Fully Adult Females

### *11.4.1 Maternal Behavior*

Most female Japanese macaques experience their first parturition at the age of 5 to 7 years, with only small differences across provisioned groups (Itoigawa et al. 1992; Koyama et al. 1992; Watanabe et al. 1992). Several studies report differences in maternal behaviors between primiparous and multiparous mothers. Nakamichi et al. (2004) report inappropriate maternal behaviors by a 9-year-old primiparous mother at Katsuyama toward her neonate directly after parturition. Near the feeding site, the primiparous mother was found not to perform maternal behaviors such as licking the neonate's fur and eating the placenta, although most mothers appropriately perform these behaviors directly after parturition (Nakamichi et al. 1992, 2004; Turner et al. 2010). The mother did not permit her neonate to cling to her; instead, she carried it, holding its trunk with one or both hands. The following day, however, she carried her infant ventrally and nursed it appropriately, as the other mothers did. These observations suggest that some primiparous females may show inappropriate maternal behavior toward their neonates, even within free-ranging groups, but they are very likely to change their maternal behavior quickly so that their neonates can survive (Nakamichi et al. 2004).

Nonetheless, it is a common observation that maternal attitudes toward their infants could differ between primiparous and multiparous mothers, within the normal range. Tanaka (1989) reports that at Shiga Heights a mother's parity has a great influence on mother–infant interactions. According to Suzuki et al. (1984), compared to multiparous mothers, primiparous mothers tend to spend more time in constant contact with their infants throughout the first 6 months of life, and are also more likely to perform not only protective behaviors such as restraining and retrieving infants but also negative behaviors such as pushing and biting infants, during the first 2 to 3 months of life. These actions indicate that primiparous mothers are very likely to be ambivalent or unstable in terms of maternal behavior. Hiraiwa (1981) also describes inappropriate infant-handling by primiparous mothers at Boso, such as holding an infant upside-down; it is probable that such inadequate or awkward infant-handling by primiparous mothers could result in a lowered infant survival rate. In fact, at Ryozen, Shiga Prefecture, the rate of infant mortality during the first year after birth for primiparous mothers was much higher than that for multiparous mothers (30.0% and 6.8%, respectively; Sugiyama and Ohsawa 1982); the same was also true for the Katsuyama group (12.6% and 9.7%, respectively; Itoigawa et al. 1992). Note that at Boso, the corresponding value for young orphaned mothers who had lost their mothers before reaching adulthood was much higher than that for primiparous mothers who had not (45.5% and 0%, respectively; Hiraiwa 1981).

These findings on mother–infant interactions from different free-ranging but provisioned groups of Japanese macaques indicate that a mother's parity has a great influence on maternal behavior, at least during the first several months of infant life; this holds true across different groups, but a mother's dominance and infant sex do not (see Sect. 11.2.4). However, some studies conducted on rhesus macaques may provide us with another story about maternal behaviors.

Maternal styles that can be characterized by the frequency of certain maternal behaviors, such as higher rejection rate, could bear a greater decisive influence on mother–infant relationships within the normal range. For example, Berman (1990), who observed free-ranging rhesus macaques on Cayo Santiago, reports that the rejection rates for individual mothers were consistent from infant to infant and similar to those of their own mothers, indicating that each female had her own maternal style and that it tended to be transmitted across generations. It is probable that individual females could display higher protectiveness toward their first-born infant than their second- or later-born infants, even within their own maternal style. Therefore, apparent behavioral differences in mother–infant relationships in terms of the mother's parity could appear when we compare two groups of primiparous and multiparous mothers. These findings could also be true for Japanese macaques. Similar to rhesus macaque females, Japanese macaque females are expected to have their own maternal style, with a common tendency for females to display more a protective maternal attitude toward their first offspring within their own maternal style.

Even though each macaque female has her own maternal style, each also has enough flexibility to adapt her caretaking behavior appropriately toward her infants. For example, Japanese macaque mothers were successfully providing appropriate care to infants with congenital limb malformations that resulted in impaired clinging ability (Nakamichi et al. 1983, 1997; Turner et al. 2005). Moreover, a female who had to walk bipedally because of her severely malformed forearms was able to care for her infants (Nakamichi 2002).

### 11.4.2 Infant Mortality and Maternal Responses to Dead Infants

While infant survival in a free-ranging context is largely influenced by environmental conditions such as food abundance and climate (Izawa 2009), the quality and quantity of care for infants as provided by their mothers could naturally influence infant survival. Therefore, examining infant mortality across different groups may be useful in determining intergroup differences in mothers' caretaking behaviors. This is also true for interbirth interval, because frequent rejections by the mother of her infant can accelerate the weaning process, leading to shorter interbirth intervals (Fairbanks and McGuire 1987).

As shown in Table 11.1, no clear differences were found in the infant mortality and interbirth intervals among three provisioned groups in Arashiyama, Katsuyama, and Awajishima: at all sites, those values were approximately 10% and 1.5 years, respectively. These findings correspond to there being no clear differences in mother–infant relationships across the provisioned groups. On the other hand, the rates of infant mortality for the wild populations were higher than those in the provisioned groups (Table 11.1); this difference is primarily caused by food scarcity among wild populations compared to provisioned groups. Therefore, it is expected that the caretaking behaviors of mothers are quantitatively and/or qualitatively different between wild and provisioned groups. However, behavioral observations of mother–infant pairs in the wild have been so limited that we cannot posit the presence or absence of any such differences between them.

The carriage of a dead infant by its mother seems to be a common observation among almost all researchers of Japanese macaques. This behavior is also observed among other simian primates, both in the wild and in captivity (Nakamichi et al. 1996). However, neither detailed behavioral nor demographical data on the carriage of a dead infant have been available, even for provisioned groups of Japanese macaques. Recently, however, Sugiyama et al. (2009) have reported as many as 157 cases of mothers carrying dead infants in more than 24 years of observation among provisioned groups at Takasakiyama, Oita Prefecture. Generally, 28% of infants who died within 30 days of birth were carried, whereas the corresponding value for infants who died after 1 month of life was as low as 4%, indicating that mothers were more likely to carry their dead infants when the infants died within 1 month of birth.

According to Maestripieri (2001), most cases of infant adoption occurred within the first 2–3 postpartum weeks; he also found that cross-fostering that had been conducted experimentally within the first 2 postpartum weeks had a high probability of success, and that mothers were able to distinguish their offspring from other infants within 3–4 weeks postpartum. On the basis of this evidence, Maestripieri (2001) concludes that the early postpartum weeks comprise the maternal sensitive period, during which mothers are highly motivated to care for their infants. Such enhanced postparturition maternal motivation may be prompted by neuroendocrinal changes related to late pregnancy, parturition, and lactation (Maestripieri 2001). The finding that, regardless of their ages, macaque mothers carried their dead infants most frequently when the infants died within 1 month of birth (Sugiyama et al. 2009), may support the presence of a maternal sensitive period. However, it should be noted that not all mothers necessarily carry their dead infants; among all dead infants, the overall rate of maternal carriage is only 15% (Sugiyama et al. 2009), which seems much lower than generally thought. Moreover, some mothers carried infants who died at around 1 year of age (Izawa 1987; Sugiyama et al. 2009).

**Table 11.1** Infant mortality within 1 year (%), and interbirth interval (years) in provisioned and wild groups of Japanese macaques

| Location | Arashiyama | Katsuyama | Awajishima | Ryozen | Ryozen | Yakushima | Kinkazan |
|---|---|---|---|---|---|---|---|
| Condition | Provisioned | Provisioned | Provisioned | Provisioned | After provisioning was stopped | Wild | Wild |
| Infant mortality within 1 year (%) | 10.3 | 10.2 | 10.0[a] | 18.1[b] | 27.3[b] | 25.0 | 22.7 |
| Interbirth interval (year)[c] | 1.46 | 1.58 | – | – | – | 2.24 | 2.37 |
| Source | Koyama et al. (1992) | Itoigawa et al. (1992) | Nakamichi et al. (1997) | Sugiyama and Ohsawa (1982) | Sugiyama and Ohsawa (1982) | Takahata et al. (1998) | Takahata et al. (1998) |

[a] Infants with congenital limb malformations were excluded

[b] The values did not include male infants

[c] Average interbirth interval following surviving infants

Therefore, the carrying of a dead infant might be related not only to the neuroendocrinal state of the mother within the first postpartum month but also to idiosyncratic factors such as maternal style.

### *11.4.3 Dominance Relationships Among Adult Females*

Kawamura (1958), who observed a provisioned group consisting of 29 animals at Minoo, Osaka Prefecture, in 1958, found that among 11 females over 3 years of age, a mother was dominant to her daughter in six of seven mother–daughter dyads, and that younger sisters were dominant to their older sisters in all four sister–sister dyads (Table 11.2). On the basis of these findings, Kawamura first posited two rules about dominance relationships among adult female Japanese macaques: (1) females acquire the rank just below that of their respective mothers, and (2) sisters rank in inverse order of age. These two principles have been referred to as “Kawamura’s rules.” Moreover, he noted that all individuals of one kin-group were collectively ranked above or below individuals of other kin-groups. He was unsure whether his two rules were necessarily applicable to groups much larger than the Minoo group, but Koyama (1967, 1970) confirmed the applicability of Kawamura’s rules to the Arashiyama group, which included as many as 50 adult females (Table 11.2). Twelve years after Koyama’s studies (1967, 1970), Takahata (1988, 1991) again confirmed that the dominance relationships among 62 adult females of the Arashiyama group largely followed Kawamura’s two rules, although deviations were not rare (Table 11.2).

When groups are a little larger than those just mentioned, intragroup differences in dominance relationships among adult females become apparent. In both the Katsuyama group (Nakamichi et al. 1995a) and the Shiga Heights group, which included 74 and 69 adult females, respectively (Kutsukake 2000), the dominance rank order was almost linear, and one female demonstrated constant dominance over the other female in almost all adult female dyads. On the other hand, there were not a few kin dyads whose dominance relationships did not adhere to Kawamura’s rules; they were found in middle- and low-ranking kin-groups, but rarely in high-ranking kin-groups. Moreover, females of high-ranking kin-groups were collectively ranked within their kin-groups, whereas females of middle- and low-ranking kin-groups were ranked separately from members of their own kin-groups. These differences in dominance relationships among adult females, between high-ranking kin-groups and middle- and low-ranking kin-groups, can be caused by differences in cohesiveness among female relatives, which can in turn be assessed in terms of behaviors such as social grooming. In fact, the grooming interactions of females in high-ranking kin-groups at Katsuyama were more evenly spread among related females, while females in middle- and low-ranking kin-groups tended to concentrate in a very small subset of related females (Nakamichi and Shizawa 2003). That is, females of high-ranking kin-groups, each of whom is very likely to interact with most of her female relatives via social grooming, maintained a highly cohesive matrilineal unit that could lead to stable dominance relationships among them, thus following Kawamura's rules. On the other hand, most females in middle- and low-ranking kin-groups limited their grooming to a few of their relatives, which could lead to weak kin-group cohesiveness; in turn, rank reversals between related females could easily occur, contrary to Kawamura's rules.

Two years after the study by Nakamichi et al. (1995a), a strongly linear dominance rank order was still confirmed in the same group at Katsuyama, which included 85 adult females (Nakamichi and Shizawa 2003). However, another 2 years later, when the number of adult females increased to 107, a group fission occurred, producing one main and two branched groups. Before the fission, many circular dominance relationships among females appeared in middle- and low-ranking females, indicating the disappearance of a linear dominance rank order, whereas a perfectly linear dominance rank order from the 1st to the 41st ranked female was confirmed (Nakamichi 1998).

In two groups at Takasakiyama – A and B, which contained 308 and 85 adult females, respectively – many female dyads showed indefinite or unstable dominance relationships, and no linear dominance rank orders were observed among the adult females of either group (Mori 1977).

In combining these findings on dominance relationships among adult females across Japanese macaque groups that vary in size from small to extra large, it is apparent that dominance relationships among adult females are strongly influenced by group size (see Table 11.2). In groups comprising 50 or fewer adult females, dominance relationships adhere almost perfectly to Kawamura's rules: one female is consistently dominant to the other in almost all dyads, females are collectively ranked within their kin-groups, and a clearly linear dominance rank order is apparent. However, as the number of adult females in a group increases, the number of dyads whose dominance relationships do not follow Kawamura's rules tends to increase. In groups including as many as 70 to 80 adult females, dominance relationships similar to those in smaller groups are still maintained in high-ranking kin-groups, whereas females in middle- and low-ranking kin-groups, whose dominance relationships with their female relatives tend to deviate from those expected from Kawamura's rules, were ranked separately from members of their own kin-groups. In much larger groups, a linear dominance rank order is not found, and dominance relationships remain unstable in many dyads.

These changes in dominance relationships among adult females, relative to an increase in group size, could be associated with how often females can interact with most other females in a group and the cognitive ability of Japanese macaques. Because the number of individuals that females often see or with which they directly interact can be limited, it is impossible for those in a large group not only to have frequent interactions with most other females but also to understand the social relationships between most other females; this limitation leads to difficulties in identifying all group members and confirming dominance relationships between themselves and other females, thus resulting in unstable dominance relationships among adult females. This difficulty may be the case with groups that have around 100 or more adult females.

**Table 11.2** Dominance relationships among adult females in different provisioned or wild groups of different populations

| Location | Minoo | Koshima | Awajishima | Arashiyama | | Shiga Heights | Katsuyama |
|---|---|---|---|---|---|---|---|
| Wild/provisioned | Provisioned | Provisioned | Provisioned | Provisioned | | Provisioned | Provisioned |
| The start of provisioning | 1956 | 1952 | 1967 | 1954 | | 1962 | 1958 |
| Group name | Minoo-B | Koshima | Awajishima | Arashiyama | Arashi-yama-B | Shiga A-1 | Katsu-yama-A |
| Observed year | 1958 | 1970 | 1979–1980 | 1964 | 1976 | 1998 | 1990–1991 |
| Group size | 29 | – | 145+ | 125 | About 230 | 199–218 | 215 |
| Number of adult females | 11 | 23 | 49 | 50 | 62 | 69 | 74 |
| Age in years of adult females | 4 | 5 | 5 | 4 | 6.5 | 6 | 6 |
| Dominance relationships | | | | | | | |
| Percent of dyads in which one individual consistently demonstrated dominance over the other | – | – | – | – | 97.0% | 98.9% | 99.2% |
| Linearity in dominance rank order | Yes | Yes | Yes | Yes | Yes | Yes | Yes |
| Percent of dyads in which mother is dominant to daughter | 85.70% | 83.30% | – | 100% | 89.70% | 87.10% | 88.30% |
| (Number of mother–daughter dyads) | ($n=7$) | ($n=6$) | – | ($n=60$) | ($n=29$) | ($n=31$) | ($n=21$) |
| Percent of dyads in which younger sister is dominant to elder sister | 100% | 84.60% | – | 100% | 72.70% | 72.20% | 75.00% |
| (Number of sister–sister dyads) | ($n=4$) | ($n=13$) | – | ($n=28$) | ($n=44$) | ($n=36$) | ($n=28$) |
| Collective ranking of related females | | | | | | | |
| High-ranking kin-groups | Perfect | High | – | Perfect | High | High | High |
| Middle- or low-ranking kin-groups | Perfect | High | – | Perfect | Partially dispersed | Low | Low |
| Source | Kawamura (1958) | Mori et al. (1977) | Nakamichi (1981) | Koyama (1967) | Takahata (1988) | Kutsukake (2000) | Nakamichi et al. (1995a) |

| Katsuyama | | Takasakiyama | | Yakushima | | | | Kinkazan |
|---|---|---|---|---|---|---|---|---|
| Provisioned | | Provisioned | | Wild | | | | Wild |
| 1958 | | 1952 | | – | – | – | - | - |
| Katsuyama-A | Katsuyama-A | Takasakiyama-B | Takasakiyama-A | P | M | Nina (A) | Kw | A |
| 1992–1993 | 1995 | 1973–1974 | 1973–1974 | 1987–1989 | 1980–1981 | 2001–2002 | 2002 | 2004 |
| 229 | – | 292 | 983 | 15–17 | 27 | 25 | 55 | – |
| 85 | 107 | 85 | 308 | 6 | 7 | 8 | 20 | 17 |
| 6 | 5 | – | – | | 6 | 4 | 4 | |
| 96.7% | – | – | – | – | – | 100.0% | 100.0% | 97.3% |
| Yes | Yes (high-ranking kin groups) | No | No | Yes | Yes | Yes | Yes | Yes |
| – | – | – | – | 100% | 100% | – | – | 100% |
| – | – | – | – | ($n=5$) | ($n=2$) | – | – | ($n = 4$) |
| – | – | – | – | 0% | 0% | – | – | 50% |
| – | – | – | – | ($n=4$) | ($n=3$) | – | – | ($n = 2$) |
| – | High | – | – | – | High | – | – | High |
| – | Low | – | – | – | High | – | – | High |
| Nakamichi and Shizawa (2003) | Nakamichi (1998) | Mori (1977) | Mori (1977) | Hill and Okayasu (1995) | Furuichi (1983) | Ventura et al. (2006) | Ventura et al. (2006) | Tsuji (2007) |

Note that, in contrast to Kawamura's second rule, older sisters were dominant to younger ones on Yakushima, even though the number of adult females in a group was often fewer than 20 (Furuichi 1983, 1986; Hill and Okayasu 1995). We discuss later the dominance relationships on Yakushima (Sect. 11.5; see also Chap. 12).

In most groups other than extra-large ones, dominance relationships among adult females are usually stable for a relatively long period (Itoigawa 1997), but changes in dominance ranks sometimes occur. When a female had a long-term affiliative relationship with a high-ranking male, she could outrank not only her mother and younger sisters but also other higher-ranking unrelated females (Takahata 1991; Itoigawa 2001). Note, however, that an affiliative relationship between a female and a high-ranking male does not always guarantee the female an increase in rank (Takahata 1991). Close relationships between an immature female and a high-ranking male, such as one that provides "paternal care," may lead to her acquisition, when she grows up, of a much higher dominance rank than that expected by Kawamura's rules (Fujii 1983). We recorded at Katsuyama the case of a female from a bottom-ranking kin-group who rose in rank to a middle-ranking position after having frequent grooming interactions with and agonistic support from some members of a middle-ranking kin-group (Nakamichi, unpublished obervations), but it does seem unusual for a female to raise her rank through such an affiliative relationship with unrelated higher-ranking females. Although a female usually rises in rank independently of her relatives (Mori et al. 1977), almost all female relatives raise their ranks collectively at times, which may result in a group fission (Koyama 1970; Oi 1988; Itoigawa 1993).

### *11.4.4 Grooming Relationships Among Adult Females*

It has been a common observation that grooming is kin biased and mainly directed up the hierarchy in Japanese macaques. At Katsuyama, the percentage of grooming bouts occurring among relatives of the total number of bouts was 57.6% in 1966–1967, 63.3% in 1977–1978, and 64.9% in 1992–1993 (Oki and Maeda 1973; Ando 1982; Nakamichi and Shizawa 2003), respectively. The corresponding values were 67.9% at Arashiyama (Koyama 1991), and 65% and 92% in wild groups on Kinkazan Island and Yakushima, respectively (Takahashi and Furuichi 1998). These values indicate the tendency for grooming to be kin biased at a group level, but this does not necessarily mean that all individuals of the group preferentially groom relatives. Rather, a Japanese macaque group may include some females who have grooming interactions with unrelated females more frequently than with their related ones. In fact, when grooming bouts among 85 adult females belonging to 16 kin-groups at Katsuyama were analyzed at an individual level, the following were found: a larger number of females showed tendencies for grooming to be kin biased and to be directed up the hierarchy, whereas at least one female in most kin-groups had grooming interactions with unrelated females as often as or more than with related females; and there was also a tendency for grooming to be directed down the hierarchy or to be well balanced (Nakamichi and Shizawa 2003).

The Japanese macaque is categorized as a despotic species among *Macaca* species, in terms of its dominance styles (Matsumura 1999; Thierry 2000; see also Chap. 12). The findings that a large number of females of the Katsuyama group showed tendencies for grooming to be kin biased and directed up the hierarchy corresponded exactly to the fact that the Japanese macaque is despotic. On the other hand, another finding was that the group included some females who showed an egalitarian tendency: grooming was directed down the hierarchy or was well balanced, and it was directed toward unrelated females as often as or more often than toward related females. Females showing such an egalitarian tendency were limited to a small number in each kin-group, but their very presence could play a role in tying together different kin-groups, thus maintaining and promoting the integrity and cohesion of a large group (Nakamichi and Shizawa 2003; see also Topic 7 by Kutsukake).

Biological market theory considers grooming a tradable commodity that can be exchanged either for itself or for other goods, such as various kinds of social tolerance (Barrett et al. 1999). In fact, some studies provide evidence for temporal or short-term relationships between grooming and grooming (Muroyama 1991), or between grooming and other goods such as access to newborn infants (Muroyama 1994; Henzi and Barrett 2002) or a reduction in aggression (Schino et al. 2005). On the other hand, in some female dyads, grooming relationships have continued for years; some other ideas are needed to explain their existence. Nakamichi and Yamada (2007) analyzed the grooming interactions of 18 Japanese macaque adult females who were studied twice, 10 years apart, at Katsuyama. Most females had frequent grooming interactions with closely related females in each of the two observation years; at the same time, they maintained grooming interactions with a few of the same unrelated females in both the first and second observation years. Females tended to maintain long-term grooming relationships for years with unrelated females who were similar to themselves in terms of dominance rank and/or age. On the other hand, long-term grooming relationships were also observed in some dyads where dominance rank reversals occurred between the two females or the dominance rank difference between them was large. It might be difficult to explain the continuity of grooming relationships in these dyads by virtue of biological market theory (Nakamichi and Yamada 2007). Moreover, in some mother–adult daughter dyads in which a daughter outranked her mother, the two individuals continued to select each other as the most frequent grooming partner, both before and after the dominance rank reversal (Nakamichi, unpublished data). Along with biological market theory, therefore, we need to consider other concepts, such as long-term psychological bonding or friendly relationships, to fully understand the existence of long-term affiliative relationships among females.

An episode of social grooming usually includes two animals, one of which is a groomer and the other, a groomee; grooming episodes simultaneously involving three or more animals are much less likely to occur. For example, in the Katsuyama group, the percentage of grooming bouts involving three or more females of the total of all bouts is less than 5% (Nakamichi, unpublished data); this may be

**Fig. 11.2** A grooming group consisting of four adult females and one adult male (*right*), in the Awajishima group of Japanese macaques

because, when two animals simultaneously groom a third one, it is not easy for the subordinate of the two groomers to continue grooming her desired target (i.e., the groomee or the third animal) while maintaining proximity to the dominant who is also grooming the same desired target. However, in the Awajishima group, it may not be unusual to observe grooming interactions simultaneously involving three or more adult females, although quantitative grooming data are not available (Fig. 11.2; Nakamichi and Turner, personal observation). Relatively frequent occurrences of grooming bouts involving three or more individuals indicate that females on Awajishima are so tolerant that they can remain proximate or maintain contact with each other, even when their dominance relationships are clear (Nakamichi 1981).

## 11.5 Tolerance Trait for Female Social Relationships in Yakushima and Awajishima Groups

In this chapter, we describe the female social development of Japanese macaques from infancy to adulthood, on the basis of literature involving free-ranging and provisioned groups, or wild groups; in so doing, we paid attention to intraspecific differences, but we found neither qualitatively nor quantitatively large differences across different macaque groups inhabiting a variety of habitats, with the exceptions of the following two points.

First, at Yakushima, in contrast to Kawamura's second rule, among sisters, the older was dominant to the younger (Furuichi 1983, 1986; Hill and Okayasu 1995), and the grooming time from dominants to subordinates and from subordinates to dominants did not differ (Hanya et al. 2008; see also Ventura et al. 2006). However, other characteristics of female social relationships at Yakushima were largely similar to those in other populations: the dominance rank order was linear, the mother was dominant to her adult daughter(s), and grooming was kin biased (see Table 11.2;

Furuichi 1986). Second, at Awajishima, females showed high levels of gregariousness without frequent agonistic interactions (Koyama et al. 1981); grooming bouts simultaneously involving at least three animals may occur relatively frequently (Nakamichi and Turner, personal observation), while a linear dominance rank order among adult females was confirmed. Unfortunately, it cannot be confirmed whether dominance relationships followed Kawamura's rules, because known kin relationships among adult females were very limited in this group.

Nakagawa (see Chap. 12), who surveyed the literature on different populations of Japanese macaques, found that macaques at Yakushima and Awajishima were considered tolerant in terms of social relationships, compared to other populations; he also points out probable phylogenetic, genetic, and socioecological causes thereof (see also Topic 1). Here, we suggest possible causes for the lack of a "youngest ascendancy" at Yakushima and the tolerant behavioral tendency at Awajishima, both from a developmental aspect.

In "youngest ascendancy," a younger sister can acquire a dominant position over her sister(s) with her mother's support (Kawai 1958; Kawamura 1958). However, if the younger sister becomes independent of her mother at a very early age, it might be impossible for her to acquire a rank position over her older sisters for lack of maternal support. It is well known that Japanese macaque mothers carry infants as old as 12 months or more, at relatively low cost; clinging to the mother's back can allow older infants or younger juveniles to satisfy psychological needs during stressful moments. Therefore, dorsal carriage by mothers could prolong affiliative mother–young offspring relationships that otherwise weaken over time (Nakamichi and Yamada 2009). As discussed earlier (Sect. 11.2.2), the dorsal carriage of infants aged around 12 months or more is usually observed in most Japanese macaque populations; the exception is Yakushima, where infants in the second half of the first year of life were infrequently found to be carried dorsally by their mothers and those in the second year of life were least likely to be so carried (Tarnaud, unpublished data). The earlier independence of an infant from its mother at Yakushima has not been confirmed with quantitative data, in terms of dorsal carriage or other behavioral indices; nonetheless, this tendency would probably explain the lack of "youngest ascendancy" in this population.

From a few months of life onward, infants at Awajishima have sometimes been seen staying in the ventral area of a female other than their mothers, without receiving rejection-related behaviors (Nakamichi 1981; Yamada, unpublished data). In other words, females permit infants of other females to enter their own ventral area, and mothers also permit their infants to make contact with other females. These affiliative interactions between infants and adult females other than their mothers have not been reported in other Japanese macaque populations. The Awajishima group is well known for having high birth rates of congenitally malformed infants (Nakamichi et al. 1997; Turner et al. 2008). Malformed infants find it difficult to spend great amounts of time with other infants in active behaviors such as social play, because of limited locomotor abilities caused by severe limb malformations; instead, they are permitted to spend a great deal of time maintaining physical contact with adult group members. This contact could lead to a relatively higher survival rate among these malformed infants; it could also promote frequent interactions with older juvenile females, in the context of infant-handling (Nakamichi et al. 1983, 1997). Therefore, it may be common for infants at Awajishima to interact affiliatively with group members other than their mothers and for adult females to permit infants to do so. Such a behavioral pattern from the early stages of development can make it possible to develop the tolerance trait, as evidenced by high levels of gregariousness, a lack of agonistic interactions, and social grooming simultaneously involving three or more individuals.

## 11.6 Aged Females

At both Arashiyama (Koyama et al. 1992) and Katsuyama (Itoigawa et al. 1992), the birth rate of female Japanese macaques from around 20 years of age decreases drastically with age, down to nil at 25 to 26 years of age. Similar to the decline in reproductive ability with increasing age, Japanese macaque females aged over 20 years are also very likely to decrease their total time spent in social interactions with other group members and increase time spent alone, showing progressively increasing social isolation with increasing age; this is the case with both the Arashiyama (Nakamichi 1984) and Katsuyama (Kato 1999; Nakamichi 2003) groups. Moreover, such an age-dependent decline in social interaction can be influenced by dominance rank and kinship: females at Katsuyama were more likely to concentrate their grooming interactions on related females with increasing age, and this tendency was more apparent in low-ranking females (Nakamichi 2003). Mitani (1986) also reported that elderly matriarchs in a wild group at Yakushima tended to cease grooming interactions with unrelated females but still continued coo call exchanges with them. Therefore, progressively increasing social isolation with increasing age is observed in terms of visually overt behaviors that accompany tactile interactions such as grooming, but elderly individuals could maintain a level of sociability equal to that from their youth, using other channels that require much less energy, such as vocal interactions.

Decreases in rank or rank reversals may occur with old age. At Arashiyama, two elderly females (i.e., more than 25 years of age) who were in the postreproductive period were outranked by some of their adult daughters, whereas females more than 20 years of age and with immature offspring were not outranked by their daughters (Nakamichi 1984). At Katsuyama, a female maintained her alpha position among adult females until her death at 32 years of age, without being outranked by her mature daughters (Itoigawa, personal communication). Her youngest daughter, who inherited the alpha position at 16 years of age, maintained the alpha position for 16 years until her own death at 32 years of age; at the time of death, she had been nonreproductive for 11 years (Nakamichi, unpublished). The oldest individuals at Katsuyama were 32 years of age; most of the elderly Japanese macaque mothers could maintain their dominance over their daughters, so long as they were in a sufficiently healthy condition to guarantee a daily social life in a group.

According to the “grandmother hypothesis,” postreproductive females can improve the survival of their grandchildren; this in turn enhances the reproductive success of their children, and thus their own inclusive fitness (for a review, see Fedigan and Pavelka 2007). In humans, midlife termination of reproductive ability in females, which does not occur in association with the advanced deterioration of the organism, is universal. Further, in humans, there is sufficient evidence to suggest that postreproductive grandmothers play an important role in the survival of their grandchildren (see Fedigan and Pavelka 2007); in nonhuman primates, however, postreproductive grandmothers are very rare, and the applicability of the grandmother hypothesis to nonhuman primate females is controversial (Fedigan and Pavelka 2001, 2007). Nonetheless, Nakamichi et al. (2010) reports two cases in the Katsuyama group in which elderly grandmothers without dependent offspring played an active role in the survival of their physically and/or psychologically dependent grandchildren. In one case, a 24-year-old grandmother provided essential care (such as holding and carrying) that ensured the survival of her 2-month-old granddaughter for a 6-day period during which the mother had temporarily disappeared for unknown reasons. The grandmother allowed her granddaughter to hold her nipple in the mouth, although she could not produce milk.

In the second case, a 14-month-old granddaughter began suckling on her 23-year-old grandmother within 6 weeks of her mother giving birth to a younger sibling; milk production seemed to be induced in the grandmother within 1 month because of repeated suckling by the granddaughter. For at least 6 months, the grandmother exhibited various patterns of maternal behavior, including nursing of the granddaughter (Fig. 11.3). Most 1-year-old macaque infants cease touching their mothers’ nipples and reduce the amount of time that they spend in contact with their mothers after the birth of younger siblings, whereas some other 1-year-old infants with younger siblings display behavioral depression characterized by reduced activity (Schino and Troisi 2001). We also observed that after a younger

**Fig. 11.3** The grandmother (*left*, 23 years old) is holding her granddaughter (22 months old) while she nurses her. On the *right*, the mother, who is the grandmother’s daughter (12 years old), is nursing her 10-month-old infant

sibling was born, some 1-year-old juvenile Japanese macaques attempted to access their mothers' nipples (Yamada and Nakamichi, unpublished data); some even resumed nursing from their mothers if a newborn sibling died within 1 month of its birth (Nakamichi et al. 2004).

In the second case, the 1-year-old granddaughter frequently attempted nipple contact with her grandmother; the grandmother accepted almost all of these attempts, which led to the satisfaction of the granddaughter's psychological needs (Nakamichi et al. 2010). These results indicate that grandmothers who were probably postreproductive exhibited maternal care behaviors toward their dependent granddaughters and could thereby promote their survival. Nozaki (2009) also reports a case in which a grandmother without dependent offspring, who was not old but middle-aged, became the most frequent grooming partner of her orphaned 1-year-old granddaughter, although she did not perform maternal behaviors such as nursing and carrying.

Because it is very rare for a Japanese macaque female to become a postreproductive grandmother (Pavelka et al. 2002; see Takahata et al. 1998), these two cases might be exceptional. However, it is useful to record these rare or infrequent cases involving postreproductive females to test the "grandmother hypothesis" in terms of the degree to which grandmothers can provide sufficient maternal care to their grandchildren and to describe the flexible and idiosyncratic nature of lifetime social development among macaque females.

## 11.7 Future Research

To clarify lifetime social development among female Japanese macaques, we still need to acquire data that answer the following questions.

First, do mother–infant relationships influence infants' social relationships with group members? If so, in what ways and by how much does the maternal style of each mother influence immature female offspring in developing social relationships with group members – particularly with same- or similar-aged immature females, with some of whom they could continue interacting after maturation? It is well known that each macaque female has her own maternal style (Berman 1990), but it remains an open question whether individual differences in maternal style can lead to differences in social development among their infants.

Second, do young adult females exhibit great change in their social relationships upon giving birth to their first infants? As mentioned earlier (see Sect. 11.3), Kudo (1986) reports that after their first birth, young adult females tend to "reset" affiliative relationships with some group members that they had maintained until then and to form new ones with some other individuals. However, quantitative data on such social changes among young adult female Japanese macaques are rarely available. If the experience of the first birth can trigger an apparent change in a new mother's social relationships, we need to clarify what it is and how it benefits her.

Third is the most important task, but it is also an extremely difficult one: describing with whom and how each female interacts throughout her lifetime in her group, at least from young adulthood to old age. The present chapter mainly focused on relationships among adult females, while those between adult females and males were not addressed (see Topic 7). Takahata (1982) reports the existence of peculiar proximity relationships between some female and male Japanese macaques, and Nakamichi et al. (1995b) report that the alpha female plays a significant role in an aged alpha male's maintenance of his dominance. Moreover, Nakamichi and Yamada (2007) report that long-term grooming partnerships are often maintained for years, even between unrelated females. However, there is a dearth of sufficient quantitative data to evaluate the benefits to females of maintaining these long-term affiliative relationships, even although the existence of long-term affiliative relationships among female baboons and the adaptive significance for females have been reported (Silk et al. 2006a,b). Thus, we need to conduct longitudinal observations to exemplify with whom, how, and for how long each female maintains affiliative relationships, not only with females but also with males; we also need to examine how and with whom she forms new affiliative relationships upon losing her familiar social partners, while paying particular attention to rarely observed incidents among macaques living in complicated but well-organized groups.

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# Chapter 12: Intraspecific Differences in Social Structure of the Japanese Macaques: A Revival of Lost Legacy by Updated Knowledge and Perspective

**Naofumi Nakagawa**

## 12.1 Introduction

### *12.1.1 Interspecific Differences of Social Relationships Among Females from a Socioecological Point of View*

The current socioecological models were developed to identify the type of food competition via ecological factors affecting female social relationships in primates (Wrangham 1980; van Schaik 1989; Isbell 1991; Sterck et al. 1997). There is a slight difference among the models (see Isbell and Young 2002 for details), but rough consensus in the following scenarios. The models predict that clumped or patchy food distributions bring about within-group contests over foods, which shape a linear and stable dominance hierarchy among females. If high-quality foods are clumped in intermediate-sized patches relative to the group size, a within-group contest would predominate. Only highly competitive females and her kin would be able to monopolize food resources, sometimes through coalition among kin (i.e., nepotism). Consequently, a linear and stable dominance hierarchy (i.e., despotic) and female philopatry would evolve among females [RN, or "Resident-Nepotistic," in the terminology of Sterck et al. (1997)]. In contrast, if low-quality foods are highly dispersed or clumped in a patch large enough to accommodate all group members, a within-group scramble (not a within-group contest) would prevail, whereby all females could equally share the food resources without any coalition. As a result, a nonlinear and unstable dominance hierarchy (i.e., egalitarian) and female dispersal would evolve [DE, or "Dispersal-Egalitarian"; Sterck et al. (1997)]. Even under a weak

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within-group contest, however, female philopatric trait would evolve to defend such large food patches cooperatively against neighboring groups under severe between-group contest [RE or "Resident-Egalitarian," Sterck et al. (1997)]. Moreover, van Schaik (1989) and Sterck et al. (1997) added a fourth category (RNT, or "Resident-Nepotistic-Tolerant"). When both types of contest were severe, dominant females would become tolerant to subordinates to derive cooperative forces from them at a group encounter although linear dominance hierarchy was found among females.

To test the socioecological models, a comparison of closely related species is desirable because the phylogeny of species may also affect their social relationships. The first evidence from closely related species that supported the socioecological model was obtained from a comparison of the red-backed squirrel monkey (*Saimiri oerstedi*) and common squirrel monkey (*Saimiri sciureus*) (Mitchell et al. 1991). Red-backed squirrel monkeys subsist on fruits that are found in small patches. Females disperse and eat in solitude, resulting in no aggression over foods and the DE type of social relationships. In contrast, the closely related common squirrel monkey subsists on fruits that grow in large patches. A number of females congregate in such large patches, and resources are worth defending, which results in frequent aggression over foods and RN social relationships. Barton et al. (1996), Isbell and Pruetz (1998), Pruetz and Isbell (2000), and Korstjens et al. (2002) found a similar causal link between ecological factors and female social relationships in comparisons of the allopatric savanna baboons (chacma baboons, *Papio ursinus*, and anubis baboons, *Papio anubis*) and of sympatric guenons in Kenya (patas monkeys, *Erythrocebus patas*, and savanna monkeys, *Cercopithecus aethiops*), and of sympatric colobus (red colobus, *Procolobus badius*, and black-and-white colobus, *Colobus polykomos*), respectively (Note: female dispersal pattern did not match the prediction for the latter two combinations). Some studies targeting one species also revealed consistent link of food characteristics, strength of within-group contest, and linearity in dominance hierarchy among females (Izar 2004; Pazol and Cords 2005; Saj et al. 2007; Robbins 2008).

As already described, RN and DE could be explained well by the socioecological model. In other words, the strength of the within-group contest was proved to be a determinant of female social relationships. On the other hand, few data support that strength of between-group contest determines female social relationships (Koenig 2002; Nakagawa and Okamoto 2003). The egalitarian patas monkeys in Kenya exhibited female philopatry despite being typified by weak between-group contest (Isbell 1998), whereas the black-and-white colobus females with linear dominance hierarchy dispersed under severe between-group contest (Korstjens et al. 2002). Moor macaque (*Macaca maurus*) females exhibiting the RNT relationship rarely join in intergroup encounters, although the frequency of between-group contest was relatively high, as opposed to the socioecological model's prediction (Matsumura 1998).

### *12.1.2 Interspecific Differences of Social Relationships Among Females in the Genus Macaca from the Phylogenetic Point of View*

Thierry (2000) proposed a four-grade scale of social structure in genus *Macaca*, ranging from highly hierarchical and nepotistic societies (grade 1) to more tolerant ones (grade 4) on the basis of such traits as aggression intensity, counter-aggression, reconciliation, dominance, dominance-related asymmetry of behavior, and nepotism. Interestingly, these traits are known to covary with one another. In a grade 1 species, intense attacks by a dominant infrequently meet with counter-aggression by a subordinate. The social power of coalitions among kin frequently outweighs the fighting ability of single individuals, and asymmetry of dominance may be marked. In contrast, in a grade 4 species, less-intense attacks by a dominant frequently bring about counter-aggression and reconciliation by a subordinate. Infrequent kin-biased coalitions link to a more symmetrical tendency of behaviors.

Japanese (*Macaca fuscata*), rhesus (*Macaca mulatta*), and possibly Taiwanese (*Macaca cyclopis*) macaques are categorized as grade 1, long-tailed (*Macaca fascicularis*) and pig-tailed (*Macaca nemestrina*) macaques are grade 2, stump-tailed (*Macaca arctodes*), Barbary (*Macaca sylvanus*), lion-tailed (*Macaca silenus*), bonnet (*Macaca radiata*), possibly toque (*Macaca sinica*), Tibetan (*Macaca thibetana*), and Assamese (*Macaca assamensis*) macaques are grade 3, and eight species of Sulawesi macaques, such as Tonkean (*Macaca tonkeana*), moor, and crested (*Macaca nigra*) macaques, are considered grade 4 (Thierry 2000).

Interspecific difference in female social relationships among macaque species (RNT vs. RN) is considered to be determined by phylogeny (Matsumura 1999; Thierry et al. 2000). It should be noted that the former category exhibits less nepotism, although categories of grades 4 and 3 in Thierry's (2000) terminology approximately correspond to RNT in the terminology of Sterck et al. (1997).

### *12.1.3 Brief Historical Background for Studies on Intraspecific Differences in the Social Structure of Japanese Macaques*

At the early stage of their studies, Japanese primatologists considered intraspecific differences in the social structure of Japanese macaques not from a socioecological aspect but from a cultural point of view (Kawamura 1956; Kawai 1964; Yamada 1966, 1971; for details, see Sect. 12.2), partly because the charismatic pioneer Kinji Imanishi and his followers of the first generation shared interests in social structures and cultures (Chaps. 1 and 9; see also Yamagiwa and Hill 1998; Nakamura and Nishida 2006). Another reason is the belief of Jun'ichiro Itani (the most canonical follower) of phylogenetic determinism on social structures (Nakamura 2009).

The understanding of social structure in Japanese macaques from a socioecological aspect must await Yukimaru Sugiyama's challenging review, which was written under the influence of Wrangham's (1980) work, a precursor to an international booming of the current socioecological model (Janson 2000). Given that this work took place after abandoning or reducing the artificial food supply to provisioned groups, Sugiyama (1987, 1990) attributed infrequent occurrences of female desertion (not group fission) from the group to increased within-group scramble and contest for foods (for details, see Sugiyama and Ohsawa 1982; Fukuda 1988).

### *12.1.4 Recent Application of Socioecological Models to Intraspecific Differences in Primate Social Structure*

In recent years, the investigators have begun to apply the socioecological model to intraspecific differences in social structure. I found that patas monkeys as well as savanna monkeys exhibited despotic social relationships among females in Cameroon. Disparity in the dominance hierarchies of patas monkeys between Kenya and Cameroon were attributable to the differences in the characteristics of food resources. Although patas monkeys in Kenya subsisted on a high density of small and dispersed food resources, those in Cameroon subsisted on a low density of clumped food resources in intermediate-sized patches (Nakagawa 2008). Koenig et al. (1998) and Vogel and Janson (2007) also found a similar causal link between ecological factors and female social relationships in comparisons of Hanuman langurs (*Presbytis entellus*) and white-faced capuchin monkeys (*Cebus capucinus*) from two different populations, respectively.

As for female social relationship in macaque species, Thibetan macaques (Berman et al. 2004) and Assamese macaques (Cooper and Bernstein 2002) were "despotic" in provisioned groups although they are supposed to have a tolerant society, grade 3 (Thierry 2000). Whether these results are caused by recent changes from clumped distribution of artificial food or are representative of the species are controversial issues. If the latter point is true, it weakens the correlation between dominance style and phylogeny in macaques as described earlier in Sect. 12.1.2.

According to Sterck et al. (1997) and Thierry (2000), Japanese macaques are supposed to be RN on the basis of data on captive animals (Chaffin et al. 1995). The Japanese macaques live in a variety of habitats from Shimokita Peninsula in the north to Yakushima Island in the south. Although some of them are free-ranging but provisioned, others are wild. So far, Japanese primatologists have revealed that provisioning and/or climatic conditions, such as rainfall, snowfall, and temperature, either directly or indirectly via vegetation, cause the intraspecific differences in their ecology (see Chaps. 4 and 5).

First, we retrace the intraspecific differences in social structure of Japanese macaques at the early stage of Japanese primatology from the cultural point of view. Second, we review these, especially the dominance style among females from the socioecological aspect. Third, we reconsider the intraspecific differences in dominance style among Japanese macaque females from various aspects, including genetics. Last, we propose future work. This review attempts to combine the “ongoing” scope with “old-fashioned” ideas and to produce upcoming views of studies on intraspecific differences in social structures.

## 12.2 Intraspecific Difference in Social Structure from the Cultural Point of View at the Early Stage of Japanese Primatology

Kawai (1964) employed the following six social indexes to categorize the social structure of Japanese macaques: (1) tolerance of leader males (i.e., high-ranking males); (2) social tension; (3) strictness of dominance hierarchy among males; (4) spatial position of subleader males (i.e., middle-ranking males); (5) gregariousness of the group; and (6) the degree of double-layered (central and peripheral) spatial structure within a group. By summing up scores in each social index (total score, ITS), he categorized 18 groups of provisioned Japanese macaques into three types: type J ($2 < \text{ITS} \le 6$), type G ($-2 \le \text{ITS} \le 2$), and type A ($-6 \le \text{ITS} < -2$) (Fig. 12.1; see also Fig. 12.2 for the locations of the study sites). The Takasakiyama group is a representative of type J, which was characterized by intolerant leader males, high social tensions, strict dominance hierarchy, peripheral location of subleader males, low gregariousness of the group, and a clear double-layered spatial structure. In contrast, the Kankakei group at Shodoshima Island is a representative of type A, characterized by tolerant leader males, low social tensions, loose dominance

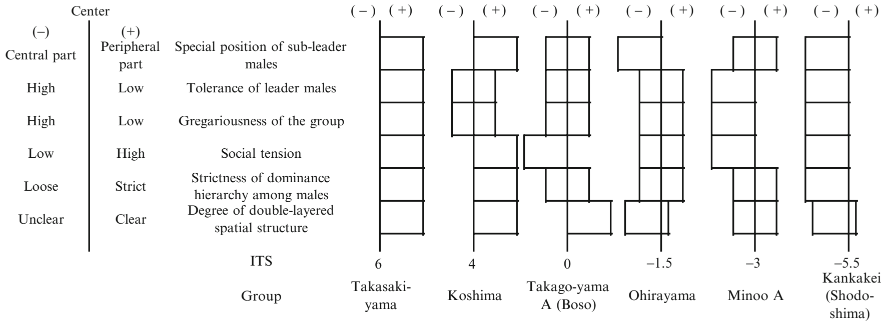

**Fig. 12.1** Categorization of the social structure of provisioned Japanese macaque groups, based on the following six social indexes: (1) tolerance of leader males (i.e., high-ranking males); (2) social tension; (3) strictness of dominance hierarchy among males; (4) special position of sub-leader males (i.e., middle-ranking males); (5) gregariousness of the group; and (6) the degree of double-layered (central and peripheral) spatial structure within a group. ITS, total summed-up scores in each social index. (Redrawn from Kawai 1964, with kind permission of emeritus Prof. M. Kawai)

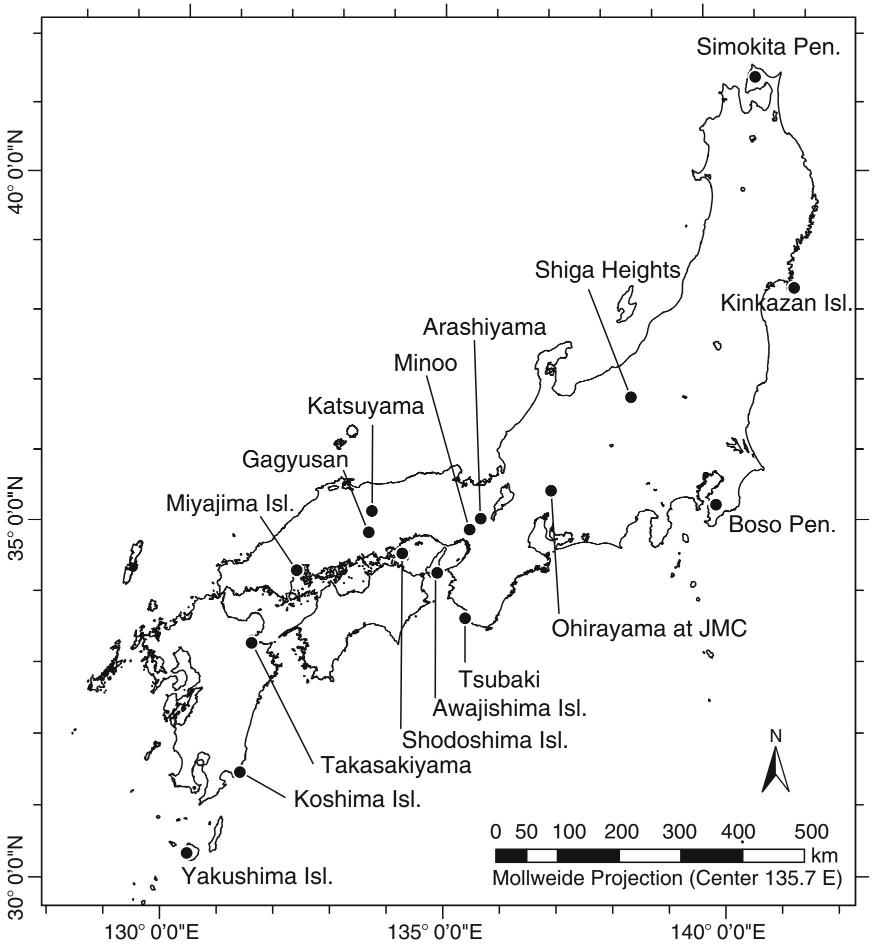

**Fig. 12.2** Locations of field research sites mentioned in this chapter. (The base map is originated from "Boundary data of cities, towns and villages of Japan ver. 6.2" by ESRI Japan Corporation, with permission)

hierarchy, central location of subleader males, high gregariousness, and unclear double-layered spatial structure.

Yamada (1971) focused on five groups at Shodoshima and examined the difference in social structure. He attempted to show gregariousness of the group on the basis of quantitative data, that is, the average area exclusively occupied by one individual, which was calculated as follows: the total area occupied by the maximum number of individuals that were simultaneously feeding on artificial foods divided by the maximum number of individuals at that time. The most gregarious Kankakei (A) group scored 0.2 $m^2$, followed by the I group (0.4 $m^2$), the T group (0.5 $m^2$), and the Chosikei (S) group (0.7 $m^2$). The least gregarious O group scored 0.9 $m^2$. According to Kawai's (1964) categorization, the only O group was classified into type G, and the remaining four groups were type A.

Koyama et al. (1981) expanded the focal population again into seven groups and examined the difference in social structure on the basis of quantitative data on social tension as well as gregariousness. The degree of gregariousness was measured by the number of individuals who were in a circle 8 m in diameter where a fixed amount of artificial foods was evenly scattered. The level of tension was measured by the frequencies of agonistic vocalizations emitted by the individuals in the circle. Surprisingly, 129 individuals were counted at maximum in the Chosikei SA group (one of the daughter groups formed by the fission of the S group), whose value corresponds to 0.39 $m^2$ in Yamada's (1971) score for gregariousness. However, only 30% of the group members were in the circle because of the large group size. In contrast, only 26 individuals (~21%) at maximum of the group members could not enter the circle in the Gagyusan group (Fig. 12.3). Combining these findings with data on level of tension on a scattergram, they found a significant positive correlation: the higher the gregariousness of the group, the higher the level of tension. Interestingly, however, the Awajishima Island group was the exceptions: low level of tension relative to gregariousness (Fig. 12.4). Given that group members usually keep a proper distance from each other to avoid

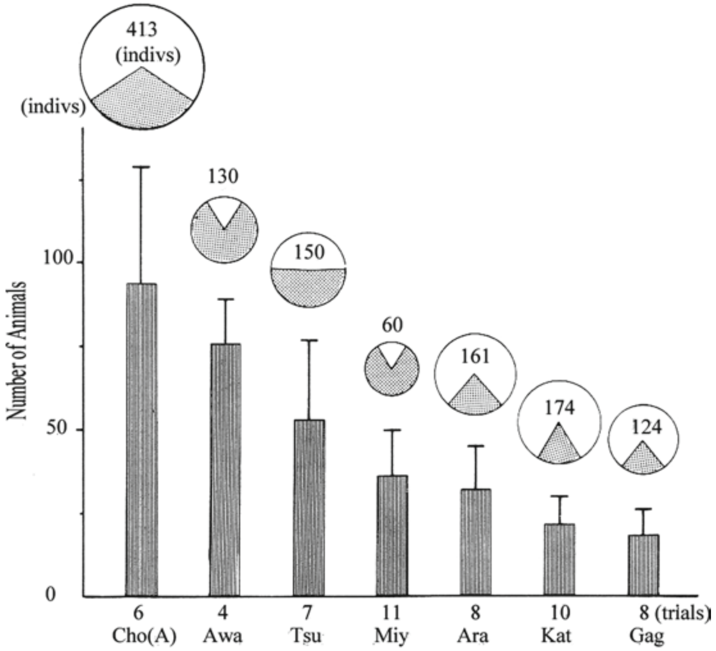

**Fig. 12.3** Maximum and mean number of individuals (*indivs*) in a circle 8 m in diameter (*columns*) and the percentage of total group members (*shaded area* of the chart) among seven provisioned Japanese macaque populations. Cho(A), Choshikei SA group at Shodoshima Island; Awa, Awajishima group at Awajishima Island; Tsu, Tsubaki group; Miy, Miyajima group at Miyajima Island; Ara, Arashiyama group; Kat, Katsuyama group; Gag, Gagyusan group. (From Koyama et al. 1981, with kind permission of Prof. T. Koyama and Springer Science+Business Media)

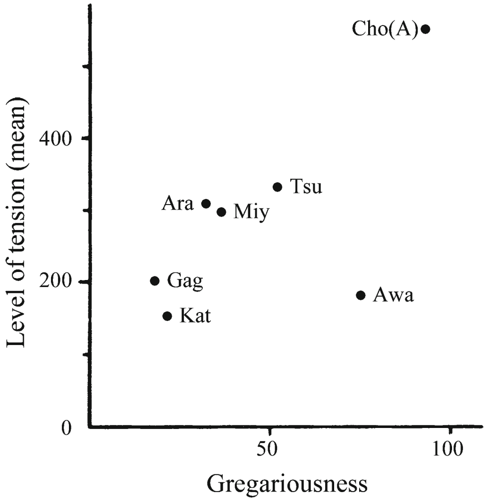

**Fig. 12.4** Correlation between gregariousness and the level of tension among seven provisioned Japanese macaque populations. Cho(A), Choshikei SA group at Shodoshima Island; Awa, Awajishima group at Awajishima Island; Tsu, Tsubaki group; Miy, Miyajima group at Miyajima Island; Ara, Arashiyama group; Kat, Katsuyama group; Gag, Gagyusan group. (From Koyama et al. 1981, with kind permission of Prof. T. Koyama and Springer Science+Business Media)

aggressions, the high gregariousness irrespective of the high level of tension in the Chosikei A group at Shodoshima also should be noted.

The intraspecific differences in social structure just described were mainly explained by three inclusive factors (see Yamada 1971 for details). (1) Personality of leader males and females. For example, the groups composed of aggressive leaders and intolerant females lead to type J. The importance of this factor was supported by the representative evidence that the social structure of the Takasakiyama group was transformed from type J into type G after the death of an aggressive alpha male. (2) Culture. The generation brought up under the influence of high-ranking or elder individuals with a certain personality would have inherited their personality. (3) Genes. A genetically tolerant personality (i.e., temperament) was selected in the Shodoshima population, which shared a limited number of sleeping sites in an area of steep cliffs.

## 12.3 Intraspecific Difference in Social Structure from the Socioecological Point of View

These studies suggested graded differences in the social structure of Japanese macaques but did not directly address dominance style among females. Kawai (1958) found a linear dominance hierarchy among adult females in the Koshima group, and the daughter's rank was determined by her mother's rank as its proximate mechanism. Kawamura (1958) also found a linear dominance hierarchy and Kawamura's rule of "youngest ascendancy" among adult females in the Minoo B group. Since then, linear dominance hierarchy among adult females and "youngest ascendancy" as its proximate mechanism have been confirmed in some other provisioned groups (Koyama 1967 for Arashiyama; Mori et al. 1989 for Koshima; Nakamichi et al. 1995 for Katsuyama; see Chap. 11), with the exception of extra-large groups, the Takasakiyama A and B groups, which consist of 300 and 100 individuals, respectively (Mori 1977a). (Note: These study groups do not include type A; sensu Kawai 1964.) Furuichi (1983), Hill and Okayasu (1995), and Hanya et al. (2008) reported a linear dominance hierarchy among adult females of wild groups, the Yakushima M, P, and H, respectively, living in warm-temperate evergreen forest, although "youngest ascendancy" was absent at least in the P group (Hill and Okayasu 1995) (see also Chap. 11). Linearity in dominance hierarchy was also found in other wild groups, the Yakushima HR group, living in coniferous forest at high altitude (Hanya et al. 2008) and the Kinkazan A group in cool-temperate deciduous forest (Tsuji 2007).

Nakagawa (1998) summarized the results of a series of comparative studies between Kinkazan macaques in cool-temperate deciduous forest and Yakushima macaques in warm-temperate evergreen forest from a socioecological point of view. Although one of the plausible determinants of female social relationships, between-group contest (van Schaik 1989; Sterck et al. 1997), was more severe in Yakusima than in Kinkazan, we have few comparable data to scrutinize the difference in the strength of within-group contest.

A decade later, Hanya et al. (2008) successfully compared food characteristics, competitive regime, and female social relationships of Yakushima macaques between two different habitat types: warm-temperate evergreen forest and coniferous forest. Between-group contest was more severe in evergreen forest than in coniferous forest, which was consistent with the prediction from food characteristics (i.e., larger fruit patch/lower density in the former). On the other hand, no difference in strength of within-group contest was found because there was no consistent difference in the rate of agonistic interactions during feeding. Moreover, no difference was found in social relationship among females: direction and concentration on particular individuals in grooming, linearity in dominance hierarchy, percentage of counter-aggression, and rate of support of juvenile by kin during agonistic interactions. Thus, they arrived at the conclusion that the female social relationships of Japanese macaques are robust and do not change according to changes in their current environment.

I agree with their conclusions on robustness of linearity in dominance hierarchy among adult females. As just described, it was found across all the groups irrespective of provisioning or vegetation of the habitats. However, such robustness is within a certain range of environment and might be lost beyond it. Table 12.1 shows comparisons of rate of agonistic interaction during feeding between nonhuman primates exhibiting despotic society (i.e., strict linear dominance hierarchy), including Japanese macaques and those of egalitarian society (sensu Sterck et al.

**Table 12.1** Frequency of agonistic interactions during feeding in some Japanese macaque populations as compared with those of representative primate species as despotic or egalitarian

| Species name | Locality (country) | Dominance style | Frequency/ feeding time (h) | References |
|---|---|---|---|---|
| *Macaca fuscata yakui* | Highland Yakushima (Japan) | Despotic | 2.98 | Hanya et al. (2008) |
| *M. fuscata yakui* | Lowland Yakushima (Japan) | Despotic | 0.49 | Hanya et al. (2008) |
| *M. fuscata yakui* | Lowland Yakushima (Japan) | Despotic | 3.16 | Hill and Okayasu (1995) |
| *M. fuscata yakui* | Lowland Yakushima (Japan) | Despotic | 0.3 | Furuichi (1983) |
| *M. fuscata fuscata* | Koshima (Japan) | Despotic | 27.2[a] | Mori (1977b) |
| *M. fuscata fuscata* | Koshima (Japan) | Despotic | 1.8[b] | Mori (1977b) |
| *M. fuscata fuscata* | Kinkazan (Japan) | Despotic | 0.75 | Saito (1996) |
| *Erythrocebus patas patas* | Kala Maloue (Cameroon) | Despotic | 0.60 | Nakagawa (2008) |
| *Cercopithecus aethiops tantalus* | Kala Maloue (Cameroon) | Despotic | 0.47 | Nakagawa (2008) |
| *E. patas pyrrhonotus* | Laikipia (Kenya) | Egalitarian | 0.34 | Pruetz and Isbell (2000) |
| *C. aethiops pygerythrus* | Laikipia (Kenya) | Despotic | 0.17 | Pruetz and Isbell (2000) |
| *Papio anubis* | Laikipia (Kenya) | Despotic | 1.8 | Barton et al. (1996) |
| *P. ursinus* | Drakensberg (South Africa) | Egalitarian | 0.05 | Barton et al. (1996) |
| *Saimiri sciureus* | Manu (Peru) | Despotic | 2.60 | Mitchell et al. (1991) |
| *S. oerstedi* | Corcovado (Costa Rica) | Egalitarian | 0.04 | Mitchell et al. (1991) |

[a] At artificial feeding site

[b] Away from artificial feeding site

1997) (i.e., no linear dominance hierarchy). As predicted from high-quality and clumped distribution of artificial foods, the frequency of agonistic interaction at artificial feeding sites in the provisioned Koshima group was extremely high. Interactions of despotic species ranged from 0.17 to 3.16; in contrast, those of egalitarian species were below 0.1 with the exception of 0.34 for egalitarian East African patas monkeys.

In contrast with the high validity of the strength of within-group contest as a determinant of female social relationships, few data support that strength of between-group contest determines female social relationships (Koenig 2002; Nakagawa and Okamoto 2003), as described in Sect. 12.1.1. I take it for granted that Hanya et al. (2008) did not find any difference in female social relationship between the two habitats in spite of the different intensity of between-group contests.

## 12.4 Reconsideration of Intraspecific Difference of Social Structure in Japanese Macaques

### *12.4.1 Shodoshima Island Population*

Japanese primatologists focused on some provisioned groups categorized J or G (sensu Kawai 1964) (see Sect. 12.2), such as the Koshima group, Takasakiyama group, and Arashiyama group for intensive studies, although they noticed graded differences of social structure in Japanese macaques at the early stage of their work. They also started to conduct research on wild, unprovisioned groups. However, the wild population in which they are enabled to obtain quantitative data on social behavior is limited to Yakushima and Kinkazan (see Chap. 1; Yamagiwa and Hill 1998). Consequently, strict dominance hierarchy became the norm in Japanese macaques even for Japanese primatologists.

Recently, a Chinese student in Japan has uncovered a forgotten treasure of the early Japanese primatologists with the guidance of one of their heirs. Zhang and Watanabe (2007) focused on the extra-large resting cluster formation by Chosikei SA and SB groups (the daughter groups formed by the fission of S group) on Shodoshima. In winter, the mean cluster size in the SA and SB groups was 17.1 and 15.9, respectively, which were significantly much larger than those in the Takasakiyama B (4.5) and C groups (4.7), although there was no consistent difference in group size between two populations. The cluster size in Shodoshima macaques became larger under lower temperatures. In contrast, cluster sizes of the Takasakiyama macaques were not increased by temperature change, although there was no significant difference in mean and minimum temperature between the two study sites. The percentage of adult females was 43% in extra-large clusters comprising more than 51 individuals in Shodoshima macaques. Surprisingly, a maximum of 137 individuals have been seen to huddle in one cluster (Fig. 12.5). More interestingly, adult females of Shodoshima macaques displayed intense aggression accompanied by biting less frequently, and counter-aggression more frequently, than those of Takasakiyama macaques (see Table 12.2). It follows from what has been said that Japanese macaques on Shodoshima have a less despotic, more tolerant social relationship among females than is typically reported for this species. In contrast with the conclusion by Hanya et al. (2008) of social robustness in Japanese macaques (see Sect. 12.3), Zhang and Watanabe (2007) revealed social plasticity in this species. Thus, a graded difference in female social relationships, which was found from the 1960s to the early 1980s, was confirmed in more quantitative way. Such a tolerant trait has been continuously seen for at least half a century in Shodoshima macaques. However, those macaques that were removed to other habitats did not form very large clusters, according to Zhang (personal observation and personal communication). In addition, it is difficult to explain the extra-large clusters as an adaptive behavior against cold, because Shodoshima is relatively warm in the range of habitats for

**Fig. 12.5** The Chosikei SB group at Shodoshima Island forms an extra-large resting cluster formation. (Photograph by Dr. P. Zhang)

Japanese macaques. For these reasons, therefore, Zhang and Watanabe (2007) concluded that a long-lasting tendency of tolerant social relationship was a behavioral tradition among Shodoshima macaques.

### *12.4.2 Yakushima Island Population*

Based on the results of the Shodoshima population, let us think twice about female social relationships among the Yakushima population. Table 12.2 compares some of the key social traits for discriminating female social relationships among some populations of Japanese macaques. The important trait is the percentage of counter-aggression. This value of Shodoshima macaques (18.8%) narrowly reaches those of tolerant (grade 3) macaque species such as the stump-tailed and Assamese macaques. Judging from this value, not only Kinkazan macaques but also Yakushima macaques are regarded as most despotic (grade 1) macaques. However, the other important trait, the conciliatory tendency of adult females, is much higher among the Yakushima macaques (25%) than that of Shiga Heights macaques (14%). This value is lower than those of the most tolerant (grade 4) macaques, such as Tonkean and moor macaques, but is equivalent to those of grade 3 macaque species, such as stump-tailed and Barbary macaques. Although there are only a few comparable data from the wild population in Kinkazan, all the other social traits of Yakushima macaques are consistent with those of tolerant macaques species: low rate of coalition by kin, no "youngest ascendancy," and no rank-related difference in birth rate and grooming directions.

Based on their morphological features, Yakushima macaques (*Macaca fuscata yakui*) have been categorized as an endemic subspecies different from Japanese macaques in other parts of Japan (*Macaca fuscata fuscata*) (see Chap. 2). Because their unique genetic features were also confirmed (Hayaishi and Kawamoto 2006; see also Chap. 3), the tolerant social trait of Yakushima macaques might come from a genetic difference (see Chap. 11 for plausible developmental mechanisms for the lack of youngest ascendancy).

## 12.5 Future Work and "Upcoming" Scope of Intraspecific Difference of Social Structure in Japanese Macaques

We found that female social relationships of Japanese macaques are robust in terms of linear dominance hierarchy but plastic in terms of tolerance to subordinates by dominant individuals. However, comparable data are needed to confirm the graded difference from intolerant to tolerant. Specifically, filling in the blank columns in Table 12.2 should be done, especially (1) the percentage of intense aggression in Yakushima; (2) the percentage of intense aggression, coalitional tendency, and rate of coalition by kin in Kinkazan; and (3) coalitional tendency, rate of coalition by kin, and "youngest ascendancy" in Shodoshima.

Let us turn to the population not listed in Table 12.2; the Awajishima population is noticeable in the sense that they seem to have the most tolerant trait, which was represented by a low level of tension relative to gregariousness (see Chap. 11). From the genetic point of view, the Shimokita Peninsula population, representing the northernmost distribution of Japanese macaques, is interesting because they have been isolated from other populations since ancient times (Kawamoto et al. 2008; see also Chap. 3). Although the Awajishima and Shimokita Peninsula populations are renowned as subjects for studies on congenital malformed macaques (Nakamichi et al. 1997; Turner et al. 2008) and feeding ecology (Watanuki et al. 1994; Nakayama et al. 1999; see also Chap. 5), respectively, sociological studies on female relationships have rarely been conducted.

When we examine the intraspecific difference in female social relationships, one of the strong points for Japanese macaques as a subject is the mass of genetic knowledge. One example is the phylogenetic relationships among populations based on mitochondrial DNA (mtDNA) from 135 localities across Japan (Kawamoto et al. 2007; see also Chap. 3). Although the tolerant traits of Yakushima and Awajishima macaques corresponded to a unique feature of mtDNA, those in Shodoshima macaques did not. Another example is the interpopulation difference in behavior-related candidate genes, which study has been just started in Japanese macaques. Interestingly, genes related to low aggressiveness were found only in the most tolerant Awajishima population of eight localities including Takasakiyama, Koshima, and Arashiyama (see Topic 1). It is hoped that data from the Yakushima and Shodoshima populations will appear in the near future.

**Table 12.2** Comparison of some of key social traits for discriminating social category among some populations of Japanese macaques

| | Lowland Yakushima (evergreen forest) | Highland Yakushima (coniferous forest) | Kinkazan |
|---|---|---|---|
| Wild/provisioned | Wild | Wild | Wild |
| Neighboring groups | Yes | Yes | Yes |
| Between-group contest | Intense | Less intense | Less intense |
| Percentage of intense aggression | – | – | – |
| Percentage of counter-aggression | 4.5%, 0.3% | 0% | 0.01% |
| Rate of coalition by kin | 0/h, 0.017/h | 0.00065/h | – |
| Conciliatory tendency of adult females | 25% | – | – |
| Rank-related difference in feeding success | – | – | Yes |
| Rank-related difference in birth rate | No | – | Yes, No |
| Rank-related difference in grooming directions | No | No | No |
| "Youngest ascendancy" | No | – | Yes |
| Day resting cluster size | – | – | – |
| References | Hill and Okayasu (1995), Saito et al. (1998), Takahata et al. (1998), Takahashi and Furuichi (1998), Majolo et al. (2005), Hanya et al. (2008) | Hanya et al. (2008) | Saito (1996), Saito et al. (1998), Takahata et al. (1998), Takahashi and Furuichi (1998), Tsuji (2007), Fujita (2008), Nakagawa (unpublished) |

[a] Stump-tailed (*M. arctodes*), Barbary (*M. sylvanus*), lion-tailed (*M. silenus*), bonnet (*M. radiata*), possibly toque (*M. sinica*), Tibetan (*M. thibetana*), and Assamese (*M. assamensis*) macaques; for grades, see text

[b] Eight species of Sulawesi macaques, such as Tonkean (*M. tonkeana*), moor (*M. maura*), and crested (*M. nigra*) macaques (Thierry 2000); for grades, see text

| Shiga Heights | Takasakiyama | Shodoshima | Grade 3 macaques[a] | Grade 4 macaques[b] |
|---|---|---|---|---|
| Provisioned | Provisioned | Provisioned | – | – |
| Yes | Yes | Yes | – | – |
| – | – | – | – | – |
| – | 5.60% | 2.50% | Low | Low |
|  | 9.0% | 18.8% | About 17–41% | About 49–68% |
| – | – | – | Low | Low |
| 14% | – | – | About 20–66% | About 48–51% |
| – | Yes | – | No | No |
| – | Yes | – | No | No |
| – | – | – | No | No |
| – | – | – | No | No |
| – | 4.5, 4.7 | 17.1, 15.9 | – | – |
| Kutsukake and Castles (2001) | Soumah and Yokota (1991), Soumah (1993), Zhang and Watanabe (2007) | Zhang and Watanabe (2007) | Thierry (2000), Thierry et al. (2000, 2008) | Thierry (2000), Thierry et al. (2000, 2008) |

We are herewith turning back to the socioecological point of view. It seems to be a hasty conclusion that we completely rule out the possibility of socioecological explanations for tolerant traits found in three populations (Awajishima, Shodoshima, and possibly Yakushima). Inoue-Murayama et al. (see Topic 1) suggest that genes related to low aggressiveness in Awajishima might be the result of selection in the past. These three populations have a common environmental characteristic, that is, small islands potentially covered with warm-temperate evergreen forest. As might be the case with the lowlands of Yakushima (see Sect. 12.3), dominant females might become tolerant to subordinates to derive cooperation from them under a strong between-group contest condition.

As for Yakushima macaques in coniferous forest under a weak between-group contest condition, we have few data for their tolerant trait other than the low rate of coalition by kin (see Table 12.2). Even if they have the same tolerant trait as in evergreen forest, such an inconsistency could be explained as "evolutionary disequilibrium" caused by recent ecological change (van Schaik and Kappeler 1996). Low overall diversity and biased geographic distribution of haplotypes of mtDNA suggested that Yakushima macaques experienced a population crash caused by volcanic activity near the island around 7,300 years ago and consequently extended their distribution from lowland evergreen forest to coniferous forest at high altitude (Hayaishi and Kawamoto 2006). There might not have been enough time for the intolerant trait to evolve for Yakushima macaques in coniferous forest.

Last, we touch upon the possibility that interpopulation differences in female social relationship can be explained by behavioral tradition. Many primatologists usually depicted the observed interpopulation behavioral differences as cultural or traditional phenomena by ruling out two other possibilities, that is, genetic and ecological explanations (Whiten et al. 1999; see also Chap. 9). In this point, Japanese macaques are suitable subjects for proving a cultural difference in social structures because genetic and ecological data have been accumulated. It is a long route to obtain evidence by the "method of elimination" (see Chap. 9). However, for Japanese primatologists at this time as well as at the early stage, cultural differences in social structure deserve an effort to prove because this seems to be a plausible scenario. According to a mathematical model by Japanese primatologists (Matsumura and Okamoto 2000), individuals that share one of two social traits, that is, despotic or tolerant, with the majority of the group members theoretically are favored over those in the minority. Thus, even nongenetic traits are maintained among populations after becoming the majority by accident. Recently, it is reported that social relationships featuring "low aggression and high affiliation" emerged after the mass mortality of group members by transmitted disease in a wild savanna baboon group and were "socially" transmitted across the generations for nearly two decades (Sapolsky 2006).

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# Part IV
# Recent Topics from Unique Approaches

# Topic 1: Behavior-Related Candidate Genes in Japanese Macaques

**Miho Inoue-Murayama, Eiji Inoue, Kunio Watanabe, Akiko Takenaka, and Yuichi Murayama**

## 13.1 Introduction

### *13.1.1 Behavior-Related Genes in Humans and Other Primates*

Both genes and the environment affect individual differences in personality (also called “behavioral traits”). In humans, about 50% of personality is estimated to be affected by an inherited factor (Ebstein 2006). Therefore, it becomes possible to understand the entire personality not only by elucidating environmental factors but also by clarifying the remaining half that is under genetic control. In humans, since the first report indicating that a novelty-seeking personality is affected by the dopamine receptor D4 (*DRD4*) genotype (Benjamin et al. 1996), various studies have shown the associations between differences in human behavioral traits and specific genotypes of neurotransmitter-related proteins: receptor, transporter, and oxidase (Ebstein 2006). However, the precise mechanism from genetic variation to personality

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variation still remains to be clarified. Furthermore, these studies are promoted mainly in common experimental animals such as knockout mice (Gardier et al. 2009) and so the results obtained seem to be not directly applicable to the direct understanding of human behaviors.

For nonhuman primates, information for the corresponding region has been accumulated. Not all the corresponding regions were polymorphic in nonhuman primate species, and the range of variation (e.g., the number of repeats) is outside that of humans (Inoue-Murayama 2009), indicating the difference in the effect of polymorphism in these species.

In the case of the serotonin transporter gene (*5-HTTLPR*), the length variation in the promoter region in rhesus macaques (*Macaca mulatta*) showed a similar tendency as in humans (Lesch et al. 1996). That is, this species has a repeat polymorphism in the region corresponding to human *5-HTTLPR*, and functional differences of each allele have shown a similar tendency as in humans (Heinz et al. 1998). Also, individuals with shorter alleles tended to display anxiety-related behavior compared with those without shorter alleles (Barr et al. 2004; Rogers et al. 2008). This polymorphism is used as the marker for considering social behavior with other measures such as plasma cortisol level (Jarrell et al. 2008), cognitive task to view photographs of high-status males (Watson et al. 2009), and gene–environment interactions (review by Suomi 2006), although the polymorphism was not observed in Japanese macaques (*Macaca fuscata*).

### *13.1.2 Polymorphic Loci in Japanese Macaques*

Records of individual behavior and regional differences in Japanese macaques have been accumulated by long-term observations and are suitable for the analysis of an inherited factor by comparison within and between groups. The results obtained may be useful for understanding human behavior.

In Japanese macaques, polymorphism was observed in monoamine oxidase A (*MAOA*) and androgen receptor (*AR*). *MAOA* degrades monoamines such as serotonin and dopamine. The promoter of *MAOA* (*MAOALPR*) includes functionally different alleles and is reported to have a relationship with aggression in humans (Alia-Klein et al. 2008) and rhesus macaques (Newman et al. 2005). Glutamine repeat in the amino acid sequence in *AR* is related to cognition (Yaffe et al. 2003), male reproduction (Mifsud et al. 2001), and aggression (Rajender et al. 2008) in humans. For *AR*, relationship with behavior has not yet been reported in nonhuman primates. All three loci are located on the X chromosome (Mifsud et al. 2001; Newman et al. 2005). Because *MAOA* degrades anxiety-related transmitter serotonin and *AR* is reported to be related to aggression in humans, as indicated above, these three genes can be candidates for aggression-related behavior in macaques.

## 13.2 Materials and Methods

### *13.2.1 Samples*

To survey regional differences, we investigated a total of 139 individuals (61 males and 78 females) from eight regions (Fig. 13.1, Table 13.1). To survey individual differences, we investigated a total of 23 males with information on dominance rank from four groups (Table 13.2).

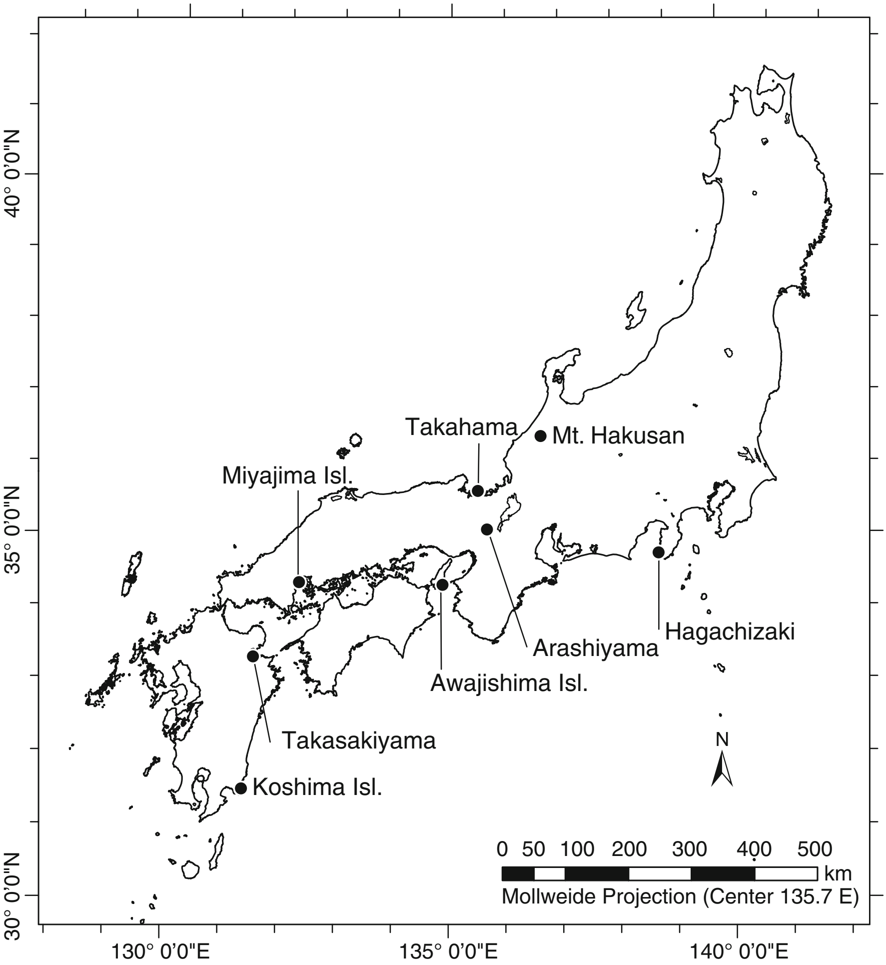

**Fig. 13.1** Location of eight regions. (The base map is originated from "Boundary data of cities, towns and villages of Japan ver. 6.2" by ESRI Japan Corporation, with permission)

**Table 13.1** Allele frequency in groups

| | *n* | | | Number of alleles | | | *He* | | | Allele frequency (*MAOALPR*) | | | Allele frequency (*AR*) | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Area | Male | Female | Total | *MAOALPR* | *AR* | Average | *MAOALPR* | *AR* | Average | 6 | 7 | 8 | 6 | 7 | 8 | 9 |
| Hakusan | 5 | 17 | 22 | 2 | 3 | 2.5 | 0.189 | 0.148 | 0.169 | 0.000 | 0.103 | 0.897 | 0.000 | 0.051 | 0.923 | 0.026 |
| Hagachizaki | 9 | 3 | 12 | 2 | 3 | 2.5 | 0.133 | 0.514 | 0.324 | 0.000 | 0.067 | 0.933 | 0.267 | 0.000 | 0.667 | 0.067 |
| Takahama | 6 | 14 | 20 | 1 | 2 | 1.5 | 0.000 | 0.401 | 0.201 | 0.000 | 0.000 | 1.000 | 0.000 | 0.000 | 0.735 | 0.265 |
| Arashiyama | 8 | 15 | 23 | 2 | 2 | 2.0 | 0.371 | 0.279 | 0.325 | 0.000 | 0.233 | 0.767 | 0.000 | 0.000 | 0.867 | 0.133 |
| Awajishima | 3 | 7 | 10 | 2 | 2 | 2.0 | 0.485 | 0.382 | 0.434 | 0.000 | 0.647 | 0.353 | 0.000 | 0.000 | 0.235 | 0.765 |
| Miyajima | 8 | 8 | 16 | 1 | 2 | 1.5 | 0.000 | 0.083 | 0.042 | 0.000 | 0.000 | 1.000 | 0.042 | 0.000 | 0.958 | 0.000 |
| Takasakiyama | 6 | 14 | 20 | 3 | 2 | 2.5 | 0.491 | 0.371 | 0.431 | 0.324 | 0.029 | 0.647 | 0.000 | 0.000 | 0.765 | 0.235 |
| Koshima | 16 | 0 | 16 | 3 | 2 | 2.5 | 0.381 | 0.125 | 0.253 | 0.071 | 0.143 | 0.786 | 0.000 | 0.000 | 0.938 | 0.063 |
| Average | 7.6 | 9.8 | 17.4 | 2 | 2.3 | 2.2 | 0.256 | 0.283 | 0.270 | – | – | – | – | – | – | – |
| Total | 61 | 78 | 139 | 3 | 4 | 3.5 | 0.319 | 0.349 | 0.334 | – | – | – | – | – | – | – |

Allele names indicate the number of repeat units

**Table 13.2** Relationship between male dominance rank and genotype (Spearman's coefficient of rank correlation, $r_s$)

| | | *MAOALPR* | | *AR* | |
|---|---|---|---|---|---|
| Group | $n$ | $r_s$ | $P$ | $r_s$ | $P$ |
| Arashiyama (PRI) | 8 | 0.630 | 0.094 | 0.158 | 0.735 |
| Koshima | 8 | –0.777 | 0.040* | –0.820 | 0.846 |

### 13.2.2 Genotyping

We amplified the polymorphic regions of two genes from genomic DNA by polymerase chain reaction (PCR) and genotyped individuals. PCR primers and genotyping procedures are described in Newman et al. (2005) for *MAOALPR* and Hong et al. (2006) for *AR*.

### 13.2.3 Data Analysis

Phylogenetic and molecular evolutionary analyses were conducted using MEGA version 4 (Tamura et al. 2007). A dendrogram of regions based on allele frequency was drawn by the neighbor-joining method (Fig. 13.2). Correlations between male dominance rank and genotypes were examined by Spearman's rank correlation test using SPSS version 17.0 (Table 13.2).

## 13.3 Results

Allele distributions of the two loci in the eight regions are shown in Table 13.1. Both loci were polymorphic, with a total number of three and four alleles observed for *MAOALPR* and *AR*, respectively. However, *MAOALPR* in Miyajima Island and Takahama were monomorphic. The average number of alleles and average heterozygosity were highest in Takasakiyama and lowest in Miyajima. Although the relationship among individuals derived from the same region is unknown, this result might reflect the large group size in Takasakiyama compared with that in the other regions (Mori 1977; Yamagiwa and Hill 1998).

Regional difference was observed in allele frequency. Awajishima Island was different from the other regions, showing a frequent short allele in *MAOALPR* and long allele in *AR* (see Table 13.1, Fig. 13.2).

Analysis of the relationship between dominance rank and genotype indicated that the short allele of *MAOALPR* was frequent in low-ranking individuals in Koshima Islet ($P < 0.05$); however, the opposite tendency was observed in Arashiyama (see Table 13.2).

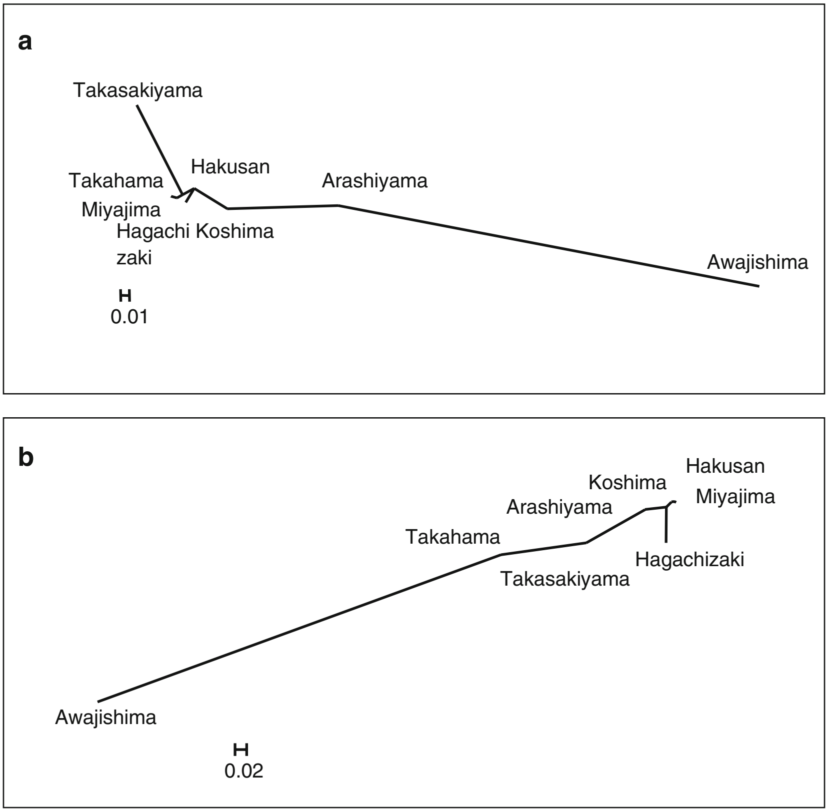

**Fig. 13.2** Neighbor-joining tree of eight regions based on allele frequencies of monoamine oxidase A (*MAOALPR*) (**a**) and androgen receptor (*AR*) (**b**)

## 13.4 General Discussion and the Way Forward

The similarity in allele distributions among regions did not correspond to the phylogeny based on blood protein polymorphism (Nozawa et al. 1991), indicating the existence of selection by genotype-specific functions of the surveyed genes. The allele frequency of *MAOALPR* and *AR* in Awajishima was different from that in other groups. Macaques in the Awajishima group are known to be highly tolerant of each other in the feeding site (Koyama et al. 1981; Fig. 13.3). The short allele of *MAOALPR* is related with low aggressiveness in rhesus macaques (Newman et al. 2005). Therefore, the frequent short alleles and high tolerance observed in Awajishima conforms to this tendency (see also Chaps. 11 and 12). The relationship between the long allele of *AR* and low aggressiveness is supported by the results in humans (Rajender et al. 2008), although the range of variation is different between Japanese macaques and humans, with all alleles in Japanese macaques being shorter than those in humans.

**Fig. 13.3** Japanese macaques in Awajishima Island, which aggregate to write a Japanese word "monkey" according to distribution of artificial foods. (Photograph courtesy of Awajishima Monkey Center)

A consistent tendency was not observed in the relationship between adult male dominance rank and genotypes. Many other environmental factors and other genetic backgrounds possibly affect dominance rank. In seasonally breeding species such as Japanese macaques, male reproductive success is not related to dominance rank (Inoue et al. 1990; Inoue and Takenaka 2008: for review, Di Fiore 2003; see also Chap. 10), indicating that being high ranking might not be fascinating to males. Furthermore, male dominance rank changes during their life (Suzuki et al. 1998). However, individual differences in personality affect the strength to strive for higher-ranking status, and such a difference in the newly immigrated male might be reflected in the speed of progression to higher dominance ranks. In contrast to males, female dominance rank does not change drastically throughout their life. As female dominance rank is matrilineal kin based and daughters inherit their mothers' dominance ranks (Koyama 1967), the genetic effect of female dominance ranks might be different from that of male dominance ranks.

For further analysis, it would be necessary to increase the number of samples and candidate genes in the future. For example, the genotype of arginin vasopressin V1a receptor is reported to affect social preference in voles (*Microtus ochrogaster*) (Hammock 2007). Because the VNTR was found in the corresponding region of Japanese macaques (Hong et al. 2009), this polymorphism is a candidate for the next survey. The study of the combined effects of several candidate loci is also a next step. With regard to behavior, more data would be required on tolerance among regional groups through individual observations. Also, various perspectives for evaluation of personality would need to be considered, such as applying the 54-point questionnaire used in apes (Weiss et al. 2009) to personality evaluation in Japanese macaques.

Studies on interspecific differences of tolerance in the genus *Macaca* have also been reported (Sterck et al. 1997; Matsumura 1999; Thierry 2000; see also

Chap. 12). Intolerant macaque species were polymorphic at *MAOALPR* (Wendland et al. 2006). Japanese macaques are categorized as an intolerant species and showed polymorphism in *MAOALPR* in our analysis. Correlation between frequency of short allele and tolerance was not observed by species comparison in macaques (Inoue-Murayama, unpublished data). A common tendency derived from comparison between species, groups, and individuals would provide us with more robust results concerning the gene basis of behavior.

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# Topic 2: Fatty Acid Content of the Plants Consumed by Japanese Macaques

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## 14.1 Introduction

The dietary crude fat content consumed by wild Japanese macaques (*Macaca fuscata*) has previously been measured from the point of view of energy balance (Iwamoto 1982; Nakagawa 1989; Soumah and Yokota 1991). However, the fatty acid contents of the foods consumed by primates including Japanese macaques have not yet been reported, even though they are nutritionally important for humans. This paper is a summary of our previous report, which was written in Japanese (Koyama et al. 2008).

### *14.1.1 Classification of Fatty Acids and Essential Fatty Acids*

Fatty acids are classified into saturated fatty acids (SFA) and unsaturated fatty acids (UFA) (Table 14.1). The UFA are further classified into monounsaturated (MUF) and polyunsaturated fatty acids (PUF) according to the number of double bonds present between their carbons. In the PUF, there are n-6 (the first double bond is

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**Table 14.1** Classification of fatty acids

| Saturated fatty acids (SFA) | Number of carbons:double bonds | |
|---|---|---|
| Lauric acid (LA) | 12:0 | $CH_3(CH_2)_{10}COOH$ |
| Myristic acid (MA) | 14:0 | $CH_3(CH_2)_{12}COOH$ |
| Palmitic acid (PA) | 16:0 | $CH_3(CH_2)_{14}COOH$ |
| Stearic acid (SA) | 18:0 | $CH_3(CH_2)_{16}COOH$ |
| Unsaturated fatty acids (UFA) | | |
| Monoenoic acid | | |
| Myristoleic acid (MLA) | 14:1n-5 | $CH_3(CH_2)_3CH{=}CH(CH_2)_7COOH$ |
| (MUF) | | |
| Palmitoleic acid (PLA) | 16:1n-7 | $CH_3(CH_2)_5CH{=}CH(CH_2)_7COOH$ |
| Vaccenic acid | 18:1n-7 | $CH_3(CH_2)_5CH{=}CH(CH_2)_9COOH$ |
| Oleic acid (OA) | 18:1n-9 | $CH_3(CH_2)_7CH{=}CH(CH_2)_7COOH$ |
| Petroselinic acid | 18:1n-12 | $CH_3(CH_2)_{10}CH{=}CH(CH_2)_4COOH$ |
| Polyenoic acid | | |
| [a]Linoleic acid (LLA) | 18:2n-6 | $CH_3(CH_2)_4CH{=}CHCH_2CH{=}CH(CH_2)_7COOH$ |
| (PUF) | | |
| [a]α-Linolenic acid (LNA) | 18:3n-3 | $CH_3CH_2CH{=}CHCH_2CH{=}CHCH_2CH{=}CH(CH_2)_7COOH$ |
| Eleostearic acid | 18:3 cis9, trans11, trans13 | $CH_3(CH_2)_3CH{=}CHCH{=}CHCH{=}CH(CH_2)_7COOH$ |
| [a]Arachidonic acid (AA) | 20:4n-6 | $CH_3(CH_2)_4CH{=}CHCH_2CH{=}CHCH_2CH{=}CHCH_2CH{=}CH(CH_2)_3COOH$ |
| Eicosapentaenoic acid (EPA) | 20:5n-3 | $CH_3CH_2CH{=}CHCH_2CH{=}CHCH_2CH{=}CHCH_2CH{=}CHCH_2CH{=}CH(CH_2)_3COOH$ |
| Docosahexaenoic acid (DHA) | 22:6n-3 | $CH_3CH_2CH{=}CHCH_2CH{=}CHCH_2CH{=}CHCH_2CH{=}CHCH_2CH{=}CHCH_2CH{=}CH(CH_2)_2COOH$ |

[a]Essential fatty acids for humans

located between the sixth and the seventh carbon from the methyl group) and n-3 (the first double bond is located between the third and the fourth carbon from the methyl group) fatty acids. Both types of fatty acids are known to have different nutritional functions, and the functions of PUF have recently been attracting interest. Animals including primates cannot synthesize PUF from SFA or MUF because they do not possess the enzymes necessary to synthesize n-6 and n-3 PUF. When animals consume linoleic acid (LLA, 18:2n-6) from plants they elongate its carbon skeleton and desaturate it in the direction of its carboxyl group to synthesize arachidonic acid (AA, 20:4n-6), and when they consume α-linolenic acid (LNA, 18:3n-3), they synthesize eicosapentaenoic acid (EPA, 20:5n-3) and docosahexaenoic acid (DHA, 22:6n-3). LLA (18:2n-6) and LNA (18:3n-3) are considered to be essential fatty acids, and AA (20:4n-6) is also an essential one because the amount of AA synthesized is not sufficient.

### *14.1.2 Importance of the (n-6)/(n-3) Ratio*

AA (20:4n-6) and EPA (20:5n-3) are precursors of eicosanoids such as prostaglandins, leukotrienes, and thromboxanes, which play several physiological roles such as in the contraction of smooth muscle, inflammation, and the coagulation of platelets. However, they compete with each other for the synthesis of eicosanoids at the level of cyclooxygenase and lipoxygenase. AA (20:4n-6) is circularized by cyclooxygenase to produce series 2 prostaglandins and thromboxanes, which show strong physiological activity, and excessive intake of n-6 PUF causes inflammation, thrombosis, and allergic reactions (Sugano 1990; Simopoulos 2002). In contrast, EPA (20:5 n-3) is a precursor of prostaglandin $I_3$, which reduces the rate of the occurrence of thrombosis by suppressing the synthesis of thromboxane$A_2$ from AA (20:4n-6) and relieving platelet aggregation (Fischer and Weber 1984). EPA (20:5n-3) is also a precursor of the series 5 leukotriene, which is a weaker inducer of inflammation and chemotactic agent than the series 4 leukotriene produced from AA (20:4n-6). The necessity of an appropriate ratio of (n-6)/(n-3) in humans is controversial. The (n-6)/(n-3) ratio is more than 15 in current European and American meals but is considered to be 1 in traditional meals from Greece (Simopoulos 2006).

### *14.1.3 The Function of DHA*

DHA (22:6n-3) is the most common fatty acid in the cerebral cortex of the brain and retina and has been studied with respect to its relationship with memory and nervous system diseases (Okuyama 1990; Sinclair et al. 2007). A large amount of DHA is required to maintain the large brain of the hominoids, but the fatty acid composition in milk is affected by the composition of fatty acids in food rather than evolutionary aspects (Connor et al. 1990; Milligan et al. 2008; Osthoff et al. 2009).

### 14.1.4 Effects of Fatty Acids on Blood Cholesterol Level

The relative content of fatty acids has been known to affect blood cholesterol level. Keys et al. (1965) reported in humans that the blood cholesterol level increases after intake of SFA and cholesterol but decreases after the intake of PUF. Hayes and Khosla (1992) carried out multiple regression analysis of the data from 227 reports and proposed the following: in the case of cholesterol intake lower than 300 mg/day, an 85.4% change is seen in blood cholesterol as a result of an increase in myristic acid (MA 14:0) and a decrease in LLA (18:2n-6). The blood cholesterol level decreases until the ratio of linoleic acid to myristic acid, LLA (18:2n-6) /MA (14:0), reaches 20 and then plateaus. Thus, it is not necessary to consume LLA (18:2n-6) above this threshold value. They also showed that palmitic acid (PA 16:0) increases the blood cholesterol level after cholesterol intake of more than 400 mg/day and that the effects of monounsaturated acid and stearic acid (18:0) are small. They confirmed a similar tendency by experimental analysis of the dietary fat of capuchins (*Cebus apella*). Takenaka et al. (2000) reported that the plasma cholesterol value was very low (75.7 ± 24.9 mg/dl) in wild Japanese macaques living on Koshima Islet compared to 158.8 ± 38.2 mg/dl in Japanese macaques bred in the Primate Research Institute, Kyoto University. Furthermore, the increase in the plasma total cholesterol was the result of an increase in low-density lipoprotein (LDL), which causes arterial sclerosis. In humans, plasma cholesterol levels lower than 160 mg/dl have been linked with increased mortality (Kannel et al. 1986).

### 14.1.5 Dietary Goal of Fatty Acids Intake for Humans (the Japanese)

In the Dietary Reference Intakes for Japanese (2005 Edition) produced by the Ministry of Health, Labor and Welfare, Japan, the tentative dietary goal for preventing lifestyle-related diseases for SFA as expressed as E% (percent of energy intake from SFA of total energy intake) was set at more than 4.5E% and less than 7.0E%, and that for n-6 PUF was set at less than 10.0E% (upper limit for men 18–69 years old: 10–12 g/day; for women 18–69 years old: 9–10 g/day), and the dietary goal for n-3 PUF was set as 50 percentile value (more than 2.6 g/day for men and more than 2.2 g/day for women). Although these values were determined by considering the amount of dietary intake by the Japanese, the (n-6)/(n-3) ratio was set at around 4.

### 14.1.6 Previous Studies of Food and Fatty Acids

The plants consumed by Japanese macaques living at several sites have been reported: Koshima (Iwamoto1982; Fukaya et al. 2002), Kinkazan Island (Nakagawa

1997b), Takasakiyama (Soumah 1992), Yakushima Island (Maruhashi 1980; Agetsuma 1995), Arashiyama, Shiga Heights, Boso Peninsula, and Shimokita Peninsula (Uehara 1977) (Table 14.2). The fatty acids included in these plants have not yet been reported except for those of several seeds (Koyama and Toyama 1956, 1957; Koyama et al. 1958, 1959; Tanaka et al. 1969, 1971; Ihara et al. 1974), even though a large amount of leaves and petals is consumed. Harwood (1980) analyzed the fatty acid contents of the leaves and roots of a few grains.

### *14.1.7 Purpose of This Study*

To assess the nutritional condition of wild Japanese macaques with regard to fatty acids, the fatty acid contents of plants eaten by them were analyzed. In this study, the fatty acid content of a total of 55 items from five parts (seeds, fruits with seeds, fruits, petals, and leaves) of 24 plant species and 3 items from 3 species as references were analyzed. The category of fruits with seeds includes nuts such as *Quercus variabilis* (No. 15) and fruits with very small seeds such as *Morus bombycis* (No. 20). The leaves and petals were found to have different fatty acid contents from all kinds of seeds and fruits (including seeds, fruits with seeds, and fruit: abbreviated as S + FS + F), which were divided into three groups. The dietary amount of fatty acids consumed per day was estimated from the present data and the nutritional analysis data of the Koshima group obtained by Iwamoto (1982) and were compared with the dietary goals for humans such as those for total fat: 20–30E%; SFA: 4.5–7E%; n-6PUF: less than 10E%; (n-6)/(n-3): 4; and LLA/MA: more than 20.

## 14.2 Materials and Methods

The materials analyzed are shown in Table 14.2, which are arranged in the order of the standardized scores of their first principal components within each of the five parts (for details, see table 4 in Koyama et al. 2008). These samples were collected in Aichi Prefecture in central Japan, and some of them were collected in different seasons. The fatty acid contents of the larva (mealworm) and imago of *Tenebrio molitor* and that of monkey chow (AS produced by Oriental Kobo) were also analyzed.

The analysis was conducted as outlined by Koyama et al. (2008). The fatty acids extracted with heptadecanoic acid as the internal standard were methylated and were analyzed by gas chromatography.

By principal component analysis (PCA), the eigen values for all principal components, their individual contribution rates to the total variance, the factor loading for the nine fatty acids, and the standardized scores for a total of the 58 plant parts were computed. A UPGMA dendrogram was drawn based on distance matrices between all the 58 plant parts computed from all eight standardized scores (Tanaka et al. 1984).

**Table 14.2** Fatty acid contents of plants

| No | Species name | Japanese name | Part | Season | Dry weight (g) | Soluble part in hexane (w/dry weight %) | Yield of fatty acid (w/dry weight %) | Fatty acid content (%) | | | | | | | | | Ref. No. |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | | LA | MA | MLA | PA | PLA | SA | OA | LLA | LNA | |
| 1 | *Dendropanax trifidus* | Kakuremino | S | Oct. L | 39.2 | 39.3 | 27.6 | 0.0 | 0.0 | 0.0 | 4.9 | 0.0 | 0.8 | [a]88.1 | 6.2 | 0.0 | 3 |
| 2 | *Aralia elata* | Taranoki | S | Oct. L | 36.8 | 17.4 | 14.1 | 0.0 | 0.0 | 0.0 | 4.6 | 0.0 | 0.9 | [a]75.8 | 18.7 | 0.0 | 2 |
| 3 | *Viburnum Awabuki* | Sangoju | S | Nov. L | 51.9 | 21.2 | 17.6 | 0.0 | 0.0 | 0.0 | 9.6 | 0.0 | 1.6 | 64.4 | 23.4 | 1.0 | 15 |
| 4 | *Clerodendron trichotomum* | Kusagi | S | Nov. L | 67.6 | 25.2 | 21.2 | 0.0 | 0.0 | 0.0 | 7.4 | 0.0 | 2.1 | 59.5 | 30.9 | 0.0 | 2 |
| 5 | *Ligustrum japonicum* | Nezumimochi | S | Jan. M | 22.8 | 14.9 | 11.0 | 0.0 | 0.0 | 0.0 | 7.7 | 0.0 | 2.8 | 55.0 | 33.3 | 1.2 | 3 |
| 6 | *Ilex integra* | Mochinoki | S | Dec. L | 59.5 | 9.4 | 8.3 | 0.0 | 0.0 | 0.0 | 7.6 | 0.0 | 2.5 | 37.3 | 52.1 | 0.5 | 2 |
| 7 | *Cinnamomum Camphora* | Kusunoki | S | Nov. M | 122.0 | 41.2 | 29.3 | 14.5 | 3.7 | 0.0 | 15.1 | 8.0 | 2.1 | 47.9 | 7.5 | 1.3 | 10 |
| 8 | *Akebia quinata* | Akebi | S | Oct. M | 50.0 | 34.8 | 26.5 | 0.7 | 0.0 | 0.0 | 27.1 | 0.0 | 2.7 | 41.2 | 28.3 | 0.0 | 7 |
| 9 | *Myrica rubra* | Yamamomo | S | Jun. M | 58.2 | 12.2 | 10.1 | 0.0 | 0.0 | 0.0 | 15.1 | 1.4 | 3.9 | 28.5 | 50.7 | 0.4 | d |
| 10 | *Eurya japonica* | Hisakaki | S | Oct. M | 21.0 | 4.5 | 3.9 | 0.0 | 0.0 | 0.0 | 8.8 | 0.0 | 2.4 | 11.4 | 76.0 | 1.4 | 2 |
| 11 | *Rhus succedanea* | Hazenoki | S | Dec. M | 51.4 | 5.8 | 5.3 | 0.0 | 0.0 | 0.0 | 16.9 | 0.0 | 4.2 | 14.1 | 64.3 | 0.5 | 2 |
| 12 | *Prunus yedoensis* | Someiyoshino | S | Jun. M | 45.3 | 10.0 | 6.4 | 0.0 | 0.0 | 0.0 | 5.5 | 0.3 | 2.2 | 20.1 | 43.9 | [b]28.1 | 9 |
| 13 | *Daphniphyllum macropodum* | Yuzuriha | FS | Dec. M | 14.9 | 9.1 | 8.4 | 0.0 | 0.0 | 0.0 | 11.8 | 0.4 | 2.9 | 60.0 | 24.1 | 0.7 | d |
| 14 | *Daphniphyllum Teijsmanni* | Himeyuzuriha | FS | Dec. E | 46.8 | 5.3 | 4.4 | 0.0 | 0.0 | 0.0 | 11.3 | 0.0 | 3.4 | 54.1 | 30.5 | 0.7 | 11 |
| 15 | *Quercus variabilis* | Abemaki | FS | Sep. L | 89.7 | 2.3 | 1.5 | 0.0 | 0.0 | 0.0 | 18.6 | 0.0 | 1.5 | 52.2 | 25.7 | 2.1 | 12 |
| 16 | *Paederia scandens* | Hekusokazura | FS | Nov. M | 44.5 | 6.1 | 2.6 | 0.0 | 1.1 | 0.0 | 14.9 | 0.0 | 2.4 | 44.4 | 34.6 | 2.5 | 2 |
| 17 | *Quercus glauca* | Arakashi | FS | Nov. M | 35.9 | 3.1 | 2.1 | 0.0 | 0.0 | 0.0 | 24.4 | 0.0 | 1.4 | 41.3 | 30.1 | 2.8 | 3 |
| 18 | *Styrax japonica* | Egonoki | FS | Jul. M | 22.9 | 7.4 | 4.6 | 0.0 | 0.0 | 0.0 | 9.0 | 0.0 | 1.5 | 27.6 | 57.5 | 4.5 | 4 |
| 19 | *Callicarpa japonica* | Murasakishikibu | FS | Dec. E | 16.4 | 9.5 | 5.4 | 0.0 | 0.0 | 0.0 | 8.4 | 0.0 | 2.8 | 12.3 | 75.4 | 1.1 | 9 |
| 20 | *Morus bombycis* | Kuwa | FS | May. L | 21.2 | 29.0 | 24.7 | 0.0 | 0.0 | 0.0 | 9.6 | 0.0 | 3.1 | 5.4 | 81.0 | 0.9 | 5 |
| 21 | *E. japonica* | Hisakaki | FS | Oct. M | 12.4 | 5.0 | 3.0 | 0.0 | 0.0 | 0.0 | 18.7 | 0.0 | 3.0 | 13.0 | 56.8 | 8.5 | 2 |
| 22 | *Podocarpus macrophylla* | Inumaki | FS | Jul. M | 100.8 | 1.9 | 0.4 | 0.0 | 0.0 | 0.0 | 37.4 | 0.0 | 4.5 | 20.4 | 23.7 | 14.0 | 3 |
| 23 | *Vaccinium bracteatum* | Shashambo | FS | Jan. M | 76.4 | 0.5 | 2.6 | 0.8 | 0.7 | 0.0 | 10.2 | 0.0 | 1.8 | 19.8 | 36.7 | 29.9 | 2 |
| 24 | *A. elata* | Taranoki | F | Oct. L | 47.2 | 6.3 | 3.8 | 0.0 | 0.0 | 0.0 | 9.1 | 0.0 | 1.4 | [a]71.1 | 18.4 | 0.0 | 2 |
| 25 | *C. trichotomum* | Kusagi | F | Nov. L | 41.6 | 10.3 | 5.8 | 0.0 | 0.0 | 0.0 | 25.9 | 2.8 | 5.5 | 60.7 | 5.2 | 0.0 | 2 |
| 26 | *D. trifidus* | Kakuremino | F | Oct. L | 48.4 | 16.4 | 12.5 | 0.0 | 0.0 | 0.0 | 31.6 | 1.3 | 2.9 | [a]41.0 | 22.7 | 0.5 | 3 |

|  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 27 | *C. Camphora* | Kusunoki | F | Nov. M | 137.0 | 29.0 | 23.8 | 21.2 | 2.9 | 0.0 | 14.5 | 6.0 | 3.0 | 37.5 | 10.4 | 4.4 | 2 |
| 28 | *L. japonicum* | Nezumimochi | F | Jan. M | 81.4 | 1.5 | 0.3 | 0.0 | 0.0 | 0.0 | 18.7 | 0.0 | 2.5 | 29.7 | 34.8 | 14.3 | 3 |
| 29 | *M. rubra* | Yamamomo | F | Jun. M | 50.0 | 7.4 | 1.3 | 0.0 | 0.0 | 0.0 | 32.7 | 0.0 | 3.7 | 19.7 | 35.7 | 8.1 | 2 |
| 30 | *I. integra* | Mochinoki | F | Dec. L | 83.5 | 1.0 | 0.3 | 0.0 | 1.5 | 0.0 | 25.4 | 2.3 | 3.2 | 20.1 | 30.0 | 17.4 | 2 |
| 31 | *R. succedanea* | Hazenoki | F | Dec. L | 22.0 | 17.0 | 15.9 | 0.0 | 0.0 | 0.0 | 78.2 | 0.0 | 5.9 | 15.9 | 0.0 | 0.0 | 2 |
| 32 | *A. quinata* | Akebi | F | Oct. M | 60.0 | 0.4 | 1.7 | 4.0 | 0.0 | 0.0 | 33.4 | 0.0 | 4.2 | 5.9 | 28.3 | 24.2 | 7 |
| 33 | *P. yedoensis* | Someiyoshino | P | Apr. M | 59.3 | 3.0 | 1.7 | 0.0 | 0.0 | 0.0 | 21.1 | 0.0 | 7.4 | 11.5 | 32.7 | 27.3 | 9 |
| 34 | *C. japonica* | Tsubaki | P | Apr. M | 10.6 | 5.7 | 2.9 | 0.0 | 0.0 | 0.0 | 31.3 | 0.0 | 1.8 | 6.7 | 33.0 | 27.1 | 3 |
| 35 | *C. japonica* | Tsubaki | L | Apr. M | 46.2 | 2.2 | 0.7 | 0.0 | 0.0 | 0.0 | 36.3 | 0.0 | 4.2 | 21.7 | 11.2 | 26.6 | 6 |
| 36 | *P. macrophylla* | Inumaki | L | Jun. L | 73.3 | 4.1 | 0.7 | 0.0 | 4.1 | 0.0 | 35.7 | 3.8 | 3.4 | 8.3 | 24.3 | 20.4 | d |
| 37 | *Q. glauca* | Arakashi | L | Nov. M | 21.0 | 5.2 | 2.2 | 0.0 | 0.0 | 0.0 | 27.0 | 0.0 | 1.5 | 7.5 | 35.5 | 28.6 | 4 |
| 38 | *C. japonica* | Murasakishikibu | L | Aug. L | 24.0 | 5.8 | 1.0 | 0.0 | 7.6 | 0.0 | 22.0 | 8.1 | 8.1 | 15.1 | 8.2 | 31.0 | 1 |
| 39 | *E. japonica* | Hisakaki | L | Oct. E | 7.4 | 8.1 | 2.1 | 0.0 | 0.0 | 0.0 | 20.4 | 6.2 | 1.6 | 15.6 | 18.3 | 38.0 | 8 |
| 40 | *I. integra* | Mochinoki | L | Oct. M | 38.4 | 9.6 | 1.1 | 0.0 | 3.3 | 7.5 | 26.8 | 7.8 | 2.4 | 8.7 | 12.3 | 31.2 | 3 |
| 41 | *M.Thunbergii* | Tabunoki | L | Dec. E | 58.2 | 4.2 | 0.4 | 0.0 | 5.0 | 0.0 | 32.0 | 0.0 | 3.6 | 7.6 | 20.0 | 31.8 | 3 |
| 42 | *C. trichotomum* | Kusagi | L | Apr. L | 70.0 | 5.4 | 1.8 | 0.0 | 1.7 | 0.0 | 26.3 | 1.8 | 3.8 | 2.3 | 31.9 | 32.2 | 2 |
| 43 | *D. macropodum* | Yuzuriha | L | Apr. M | 52.4 | 3.1 | 1.2 | 0.0 | 1.8 | 0.0 | 24.1 | 1.0 | 2.1 | 2.9 | 32.2 | 35.9 | 14 |
| 44 | *C. japonica* | Murasakishikibu | L | Jun. E | 35.3 | 6.5 | 2.4 | 0.0 | 0.7 | 0.0 | 21.4 | 3.7 | 3.0 | 11.3 | 13.7 | 46.3 | 1 |
| 45 | *S. japonica* | Egonoki | L | May. M | 30.0 | 3.2 | 0.8 | 0.0 | 0.0 | 0.0 | 39.4 | 0.0 | 2.5 | 5.8 | 13.8 | 38.5 | 4 |
| 46 | *P. yedoensis* | Someiyoshino | L | Aug. E | 34.0 | 7.1 | 1.4 | 0.0 | 4.7 | 0.0 | 20.1 | 5.1 | 4.6 | 7.4 | 13.8 | 44.2 | 13 |
| 47 | *P. scandens* | Hekusokazura | L | Nov. M | 42.0 | 4.5 | 1.1 | 0.0 | 5.6 | 0.0 | 24.0 | 0.0 | 0.0 | 7.0 | 18.5 | 44.8 | 2 |
| 48 | *C. trichotomum* | Kusagi | L | May. E | 70.0 | 5.3 | 1.7 | 0.0 | 4.0 | 0.0 | 23.1 | 4.9 | 3.3 | 1.9 | 15.5 | 47.3 | 2 |
| 49 | *P. yedoensis* | Someiyoshino | L | Apr. E | 41.2 | 6.3 | 2.4 | 0.0 | 4.6 | 0.0 | 17.0 | 0.0 | 3.6 | 1.0 | 23.7 | 50.2 | 13 |
| 50 | *D. macropodum* | Yuzuriha | L | Nov. M | 29.8 | 4.7 | 1.2 | 0.0 | 2.4 | 0.0 | 21.5 | 2.4 | 2.1 | 2.2 | 19.3 | 50.1 | 14 |
| 51 | *D. Teijsmanni* | Himeyuzuriha | L | Dec. M | 24.1 | 4.5 | 0.8 | 0.0 | 7.6 | 0.0 | 19.7 | 3.4 | 2.2 | 2.4 | 15.0 | 49.8 | 2 |
| 52 | *P. yedoensis* | Someiyoshino | L | Jul. E | 37.1 | 5.4 | 4.2 | 0.0 | 1.8 | 0.0 | 22.1 | 1.4 | 4.3 | 3.0 | 15.3 | 52.1 | 13 |
| 53 | *E. japonica* | Hisakaki | L | Apr. M | 41.3 | 1.7 | 0.6 | 0.0 | 1.5 | 0.0 | 28.6 | 0.8 | 1.7 | 3.7 | 11.1 | 52.6 | 8 |
| 54 | *M. bombycis* | Kuwa | L | Aug. L | 46.1 | 9.1 | 1.7 | 0.0 | 3.6 | 0.0 | 21.4 | 3.6 | 4.7 | 1.9 | 10.5 | 54.2 | 5 |
| 55 | *M. bombycis* | Kuwa | L | Jul. M | 41.8 | 9.3 | 2.2 | 0.0 | 4.0 | 0.0 | 20.5 | 3.7 | 4.5 | 1.9 | 10.5 | 55.0 | 5 |
| 56 | *M. bombycis* | Kuwa | L | May. E | 24.3 | 9.1 | 4.6 | 0.0 | 1.5 | 0.0 | 13.8 | 2.3 | 2.2 | 1.5 | 17.7 | 61.1 | 5 |
| 57 | *P. yedoensis* | Someiyoshino | L | May. E | 24.3 | 10.4 | 4.3 | 0.0 | 1.4 | 0.0 | 16.8 | 2.0 | 2.6 | 0.9 | 15.9 | 60.5 | 13 |

(continued)

**Table 14.2** (continued)

| No | Species name | Japanese name | Part | Season | Dry weight (g) | Soluble part in hexane (w/dry weight %) | Yield of fatty acid (w/dry weight %) | Fatty acid content (%) | | | | | | | | | Ref. No. |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | | LA | MA | MLA | PA | PLA | SA | OA | LLA | LNA | |
| 58 | *M. bombycis* | Kuwa | L | Jun. E | 39.1 | 5.8 | 3.7 | 0.0 | 0.8 | 0.0 | 11.0 | 1.7 | 1.4 | 0.9 | 13.5 | 70.7 | 5 |
| | *Tenebrio molitor* | Chairokomenogomi | larva | | 6.3 | 35.7 | 29.3 | | 4.0 | 0.0 | 20.4 | 1.9 | 2.6 | 36.9 | 32.8 | 1.5 | |
| | | Mushi Damashi | imago | | 2.0 | 22.9 | 16.7 | | 2.4 | 0.0 | 22.0 | 1.6 | 4.9 | 41.0 | 27.4 | 0.8 | |
| | Monkey chow AS | | | | 100.0 | 10.4 | 9.8 | | 5.0 | 7.5 | 13.8 | 7.7 | 4.0 | 21.8 | 29.1 | 5.7 | [c]5.3 |

S, seeds; FS, fruits with seeds; F, fruits; P, petals; L, leaves; LA, lauric acid; MA, myristic acid; MLA, myristoleic acid; PA, palmitic acid; PLA, palmitoleic acid; SA, stearic acid; OA, oleic acid;, LLA, linoleic acid; LNA, α-linolenic acid

E, M, and L represent the early, middle, and late part of the month, respectively

1, Mori (1979); 2, Maruhashi (1980); 3, Iwamoto (1982); 4, Yokota and Hagimoto (1985); 5, Maruhashi (1988a); 6, Maruhashi (1988b); 7, Soumah and Yokota (1991); 8, Nakagawa et al. (1996); 9, Nakagawa (1997b); 10, Otani and Shibata (2000); 11, Nature Study Association of Bousou (1974); 12, Kanamori (1994); 13, Izawa and Komuro (1993); 14, Invest. Comm. of *Macaca fuscata yakui* (1997); 15, Hill (1997)

[a] Petroselinic acid (18:1 n-12) instead of oleic acid

[b] Eleostearic acid (18:3 n-5 conjugated) instead of α-linolenic acid

[c] Vaccenic acid (18:1 n-7)

[d] These samples have not yet been reported as food items eaten by Japanese macaques, but different parts of the same species are known to be included in their diet

## 14.3 Results and Discussion

### *14.3.1 PCA Results*

Nine common fatty acids were detected in the 58 plants parts consumed by Japanese macaques (see Table 14.2). Furthermore, petroselinic acid (18:1n-12) was found in the seeds and fruit of two species (*Dendropanax trifidus* and *Aralia elata*), and eleostearic acid (18:3n-5 conjugated double bonds) was detected in the seeds of one species (*Prunus yedoensis*). No fatty acids with a carbon number higher than 18 such as AA (20:4n-6), which is an essential fatty acid in humans, were detected. PA (16:0) was the main component of SFA in all the five parts, and the MA (14:0) and SA (18:0) contents peaked at 8%.

Figure 14.1 shows the dendrogram drawn from the eight standardized scores of the 58 plant items (for details, see table 4 in Koyama et al. 2008). The fruits of *Rhus succedanea* (No. 31) branched away at first and was then classified into two major groups: group 1, including S + FS + F, and group 2, including all petals, leaves and some S + FS + F.

The factor loading of C18 monoenoic acid and LNA (18:3n-3) were +0.909 and −0.937, respectively, for the first principal component (individual contribution rate, 60.0%), that of LLA (18:2n-6) was +0.949 for the second principal component (individual contribution rate, 26.8%), and that of PA (16:0) was +0.897 for the third principal component (individual contribution rate, 11.3%). In Fig. 14.2a, which shows a scatter diagram with the first principal component on the horizontal axis and the second principal component on the vertical axis, S + FS + F are located on the right side (group 1 and group 2-1-1), and the petals and leaves are located on the left side (group 2). The petals and leaves contained higher amounts (20.4–70.7%) of LNA (18:3n-3), whereas the S + FS + F contained lower amounts (0–29.9%) of LNA (18:3n-3) but high amounts (5.4–88.1%) of C18 monoenoic acid. All S + FS + F were further classified into three subgroups according to their LLA (18:2n-6) content: high amount (group 1-1, 50.7–81.0%), medium amount (the same as in the leaves) (group 2-1-1, 23.7–43.9%), and low amount (group 1-2, 5.2–34.6%). The fruits of *R. succedanea* (No. 31) differed from those of the others in its PA (16:0) content (78.2%) (Fig. 14.2b), with the third principal component being shown on the vertical axis. Group 2 was divided into two subgroups, which were assigned as 2-1-1 and 2-1-2 because their branch lengths were the same as the third step of group 1 (see Fig. 14.2).

### *14.3.2 Seasonal Changes*

The seasonal changes in the fatty acid contents of the leaves of six species (*Callicarpa japonica*, *Eurya japonica*, *Clerodendron trichotomum*, *Daphniphyllum macropodum*, *Prunus yedoensis*, and *Morus bombycis*) were analyzed and are shown in Fig. 14.3a,b after being picked out from Fig. 14.2a,b, respectively. The amounts of oleic acid (OA 18:1n-9), LLA (18:2n-6), and PA (16:0) were reduced but

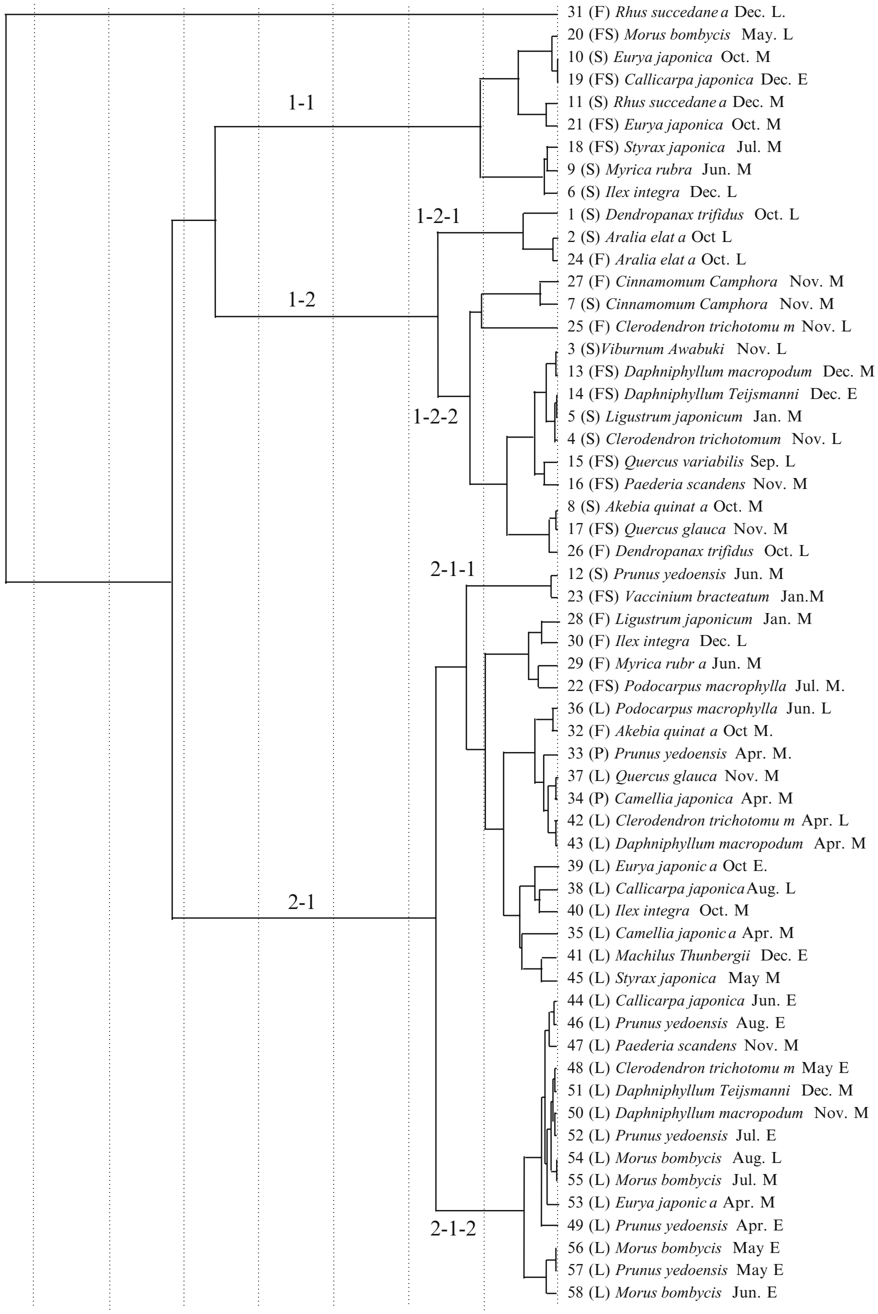

**Fig. 14.1** Dendrogram drawn by UPGMA (unweighted pair group method with arithmetic mean) based on the eight principal component scores of 58 items. (F), fruits; (FS), fruits with seeds; (S), seeds; (P), petals; (L), leaves. (From Koyama et al. 2008, with kind permission of Primate Society of Japan)

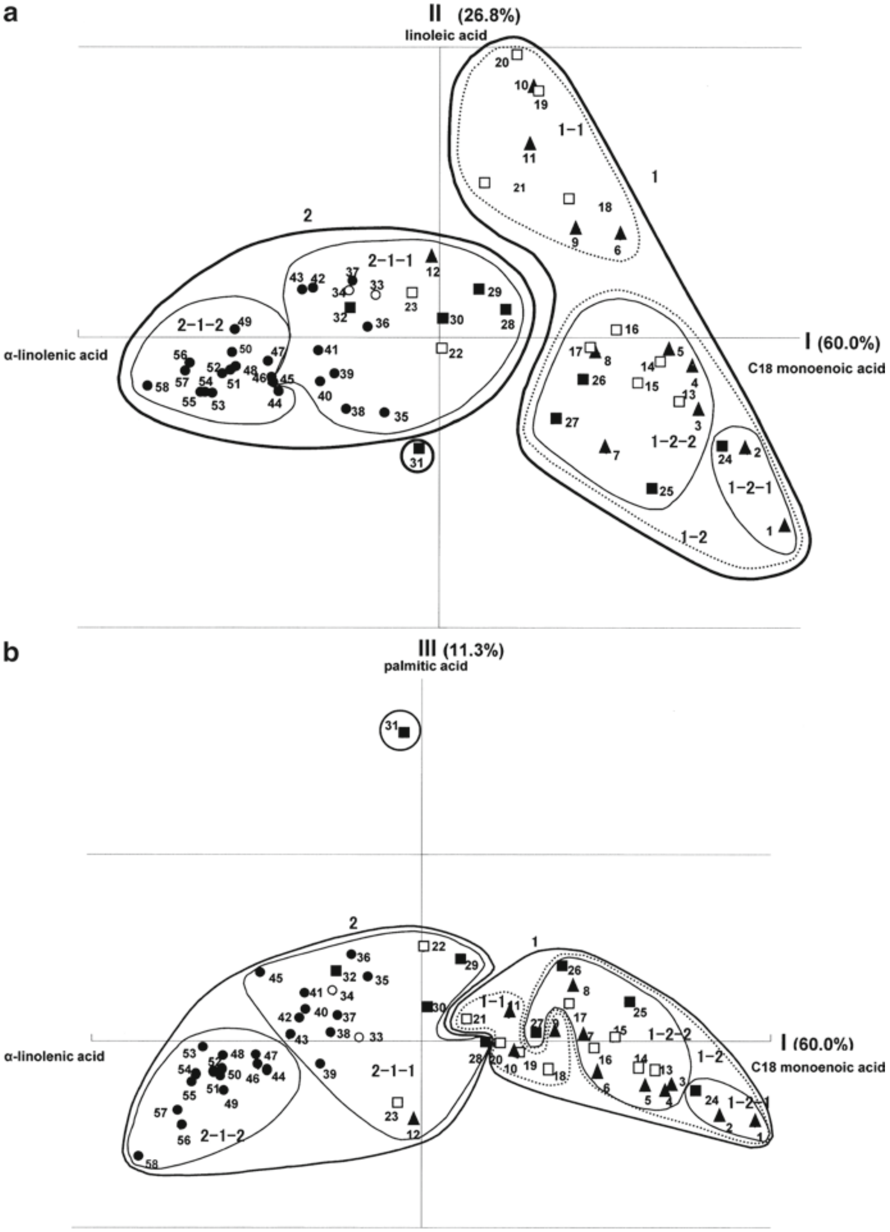

**Fig. 14.2** (**a**) Scatter diagram with the first principal component on the *horizontal axis* and the second principal component on the *vertical axis*. *Filled triangles*, seeds; *open squares*, fruits with seeds; *filled squares*, fruits; *open circles*, petals; *filled circles*, leaves. The sample numbers are the same as those in Table 2. (From Koyama et al. 2008, with kind permission of Primate Society of Japan) (**b**) Scatter diagram with the first principal component on the *horizontal axis* and the third principal component on the *vertical axis*. *Filled triangles*, seeds; *open squares*, fruits with seeds; *filled squares*, fruits; *open circles*, petals; *filled circles*, leaves. Sample numbers are the same as those in Table 14.2. (From Koyama et al. 2008, with kind permission of Primate Society of Japan)

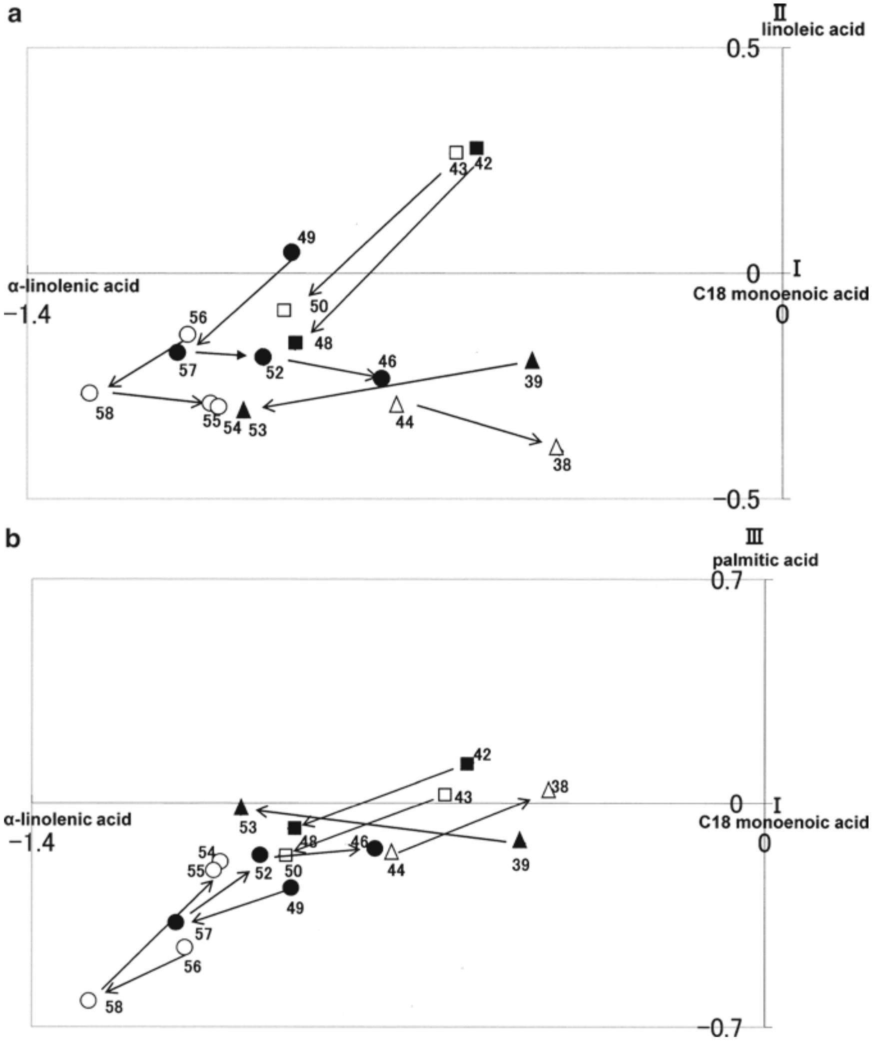

**Fig. 14.3** Seasonal changes in leaves from the results of the principal component analysis. (**a**) Scatter diagram of the first and second principal components. (**b**) Scatter diagram of first and third principal components. *Filled circles*, *Prunus yedoensis*; *open circles*, *Morus bombycis*; *filled triangles*, *Eurya japonica*; *open triangles*, *Callicarpa japonica*; *filled squares*, *Clerodendron trichotomum*, *open squares*, *Daphniphyllum macropodum.* The sample numbers are the same as in Table 14.2. (From Koyama et al. 2008, with kind permission of Primate Society of Japan)

that of LNA (18:3n-3) was increased during the first step of the progression from young to mature leaves. However, at the second step, the amount of LNA (18:3n-3) was decreased, and those of PA (16:0) and OA (18:1n-9) were increased, but that of LLA (18:2n-6) was almost unchanged. These changes were speculated to be similar to those seen in the plants that are able to attach carbons to PA (16:0) and increase the number of double bonds during the first step of the synthesis of LNA (18:3n-3), which localizes in the membrane of chloroplasts and is necessary for the photosynthesis required for the growth of young leaves. However, the amount of LNA (18:3n-3) decreased, and the amounts of other fatty acids remained constant in the mature leaves at the second step.

DHA (22:6n-3) is an important component of the brain and retina, and it is known that DHA is included in the milk of rhesus macaques (*M. mulatta*) (Milligan et al. 2008). However, as DHA was not found in the plants in the present study, macaques must synthesize DHA from LNA (18:3n-3). Since the birth season of the Koshima group was from the middle of June to early July (Watanabe et al. 1992; Mori et al. 1997), the high amount of LNA(18:3n-3) present in young leaves in this season might aid the brain development of neonate macaques.

### 14.3.3 Comparison of Fatty Acids in Seeds with Those in Fruits

In comparisons of the fatty acid contents of the seeds with those of the fruits in nine analyzed species, C18 monoenoic acid (18:1) was found in higher amounts in the seeds of all species except *R. succedanea* (Nos. 11 and 31), while LNA (18:3n-3) was found in higher amounts in fruits but in very low amounts in seeds. The amount of LLA (18:2n-6) was higher in the seeds of five species (Nos. 9 and 29, Nos. 11 and 31, Nos. 6 and 30, Nos. 2 and 24, and Nos. 4 and 25) than in the fruits, but in the other four species (Nos. 8 and 32, Nos. 7 and 27, Nos. 1 and 26, and Nos. 5 and 28), the amount in the fruits was higher than that in the seeds. Figure 14.2b shows that the amounts of PA (16:0) in the seeds and fruits of *Cinnamomum camphora* (Nos. 7 and 27) were the almost the same, but in the other eight species the amounts of PA (16:0) were higher in the fruits. The exceptions were *R. succedanea* (16.9% in seeds, No. 11, and 78.2% in fruits, No. 31) and *D. trifidus* (4.9% in seeds, No. 1, and 31.6% in fruits, No. 26).

### 14.3.4 Identification of Eleostearic Acid and Petroselinic Acid

The high refractive indexes ($n^{20}_{D} = 1.4995$ and 1.4450) of seed oil and the methylated fatty acids from *P. yedoensis* (No. 12), respectively, and the peak positions of the ultraviolet absorption spectrum of methylated fatty acid (260, 270, and 280 nm) indicated the presence of α- and β-eleostearic acids (18:3n-5).

From the melting points of the solid acids in the seed oil from *D. trifidus* (No. 1) (31°–32°C) and its elaidic acid (50°–51°C), petroselinic acid (18:1n-12) was identified. The monoenoic acid of the fruits oil from *D. trifidus* (No. 26) and of the oils from the seeds and fruits of *A. elata* (Nos. 2 and 24) were all identified as petroselinic acid (18:1n-12) by the same procedures. The retention times of oleic acid (18:1n-9) and petroselinic acid (18:1n-12) were the same under these gas chromatography conditions.

### *14.3.5 Estimation of the Intake of Fatty Acids in the Koshima Group*

It is necessary to analyze the fatty acid content in the foods at each location to compare the amount of fatty acids consumed by Japanese macaques in 1 day with the dietary goal values for humans. We estimated the daily intake of fatty acids from the data obtained in this study and the food items reported by Iwamoto (1982) at Koshima in a warm-temperate evergreen forest such as those in Aichi Prefecture.

During October to March, the Japanese macaques in Koshima consumed the greatest amount of S+ FS + F in November (dry weight content of leaves, 3.6%; that of S + FS + F, 89.0%), and they consumed the greatest amount of leaves in February (dry weight content of leaves, 74.8%; that of S + FS + F, 15.8%). Because Iwamoto (1982) also reported the total dry weight and energy intake in 1 day (in November: 272 g and 1,233 kcal; in February: 299 g and 1,173 kcal), we tried to estimate fatty acid content for November and February assuming that all leaves and all S + FS + F were consumed from one group as classified by the PCA. As shown in Table 14.3, the amount of fatty acids was estimated for six situations involving the consumption of one of the three groups of S + FS + F together with group 2-1-1 leaves or group 2-1-2 leaves in November and February; 15 and 18 items were consumed in November and February, respectively. First, we calculated the mean values for the two groups of leaves and three groups of S + FS + F (see Table 14.4) and used these data for the subsequent calculations. (If the analyzed items were included, we used each measured value.)

For every 100 g dry weight of food consumed, the consumed amount of each fatty acid in each group was calculated as follows:

$$\text{Consumed dry weight \% of each group} \times \text{total fatty acid amount \%} \times \text{each fatty acid content \%}/10{,}000$$

Since the total amount of dry weight consumed was 272 g and 299 g in November and February, respectively, the amount of each fatty acid consumed per day was calculated by multiplying by 2.72 and 2.99, respectively.

The energy content of each fatty acid was obtained by multiplying by the Atwater factor (9 kcal/g), and then the energy percent (E%) was calculated from the total energy intake. In November, E% = (amount of each fatty acid consumed per day) × 9/1,233 × 100; in February, E% = (amount of each fatty acid consumed per day) × 9/1,173 × 100.

As shown in Table 14.3, total daily fatty acid intake in November accounted for 14.6–23.6E%, which was as high as that in humans, if they ate S + FS + F from group 1-1 or group 1-2 together with any group of leaves; this was true because the amount of fat (the soluble part in hexane) included in the S + FS + F of group 1 was 2–3 times as high as that in the leaves and the amount of fatty acids in this group was 4–5 times as high as that in the leaves (see Table 14.4). The intake of LNA (18:3n-3) was increased two- to threefold in February (1.7–1.8E%) compared with November (0.3–0.7E%) as a consequence of the high intake of group 2-1-2 leaves. If all the S + F of group 1-1 was consumed in November, LLA (18:2n-6) comprised 9.3E%, which is nearly the same as the dietary goal in humans (10E%). However,

**Table 14.3** Estimated fatty acid amount eaten by the Koshima troop if they had eaten all leaves, and fruits and seeds from each group

November: If the macaques had consumed each group of S + FS + F with Group 2-1-1 leaves

| | g/day | | | E% | | |
|---|---|---|---|---|---|---|
| Fatty acid | (1-1) | (1-2) | (2-1-1 S+FS+F) | (1-1) | (1-2) | (2-1-1 F+FS+F) |
| LA (12:0) | 0 | 0.7 | 0 | 0 | 0.5 | 0 |
| MA (14:0) | 0 | 0 | 0 | 0 | 0.1 | 0 |
| MLA (14:1) | 0 | 0 | 0 | 0 | 0 | 0 |
| PA (16:0) | 2.4 | 4.9 | 1.1 | 1.7 | 3.6 | 0.8 |
| PLA (16:1) | 0 | 0.4 | 0 | 0 | 0.3 | 0 |
| SA (18:0) | 0.6 | 0.8 | 0.1 | 0.4 | 0.6 | 0.1 |
| OA (18:1) | 3.7 | 17.3 | 0.9 | 2.7 | 12.6 | 0.7 |
| LLA (18:2n-6) | 12.8 | 7.6 | 1.6 | 9.3 | 5.6 | 1.1 |
| LNA (18:3n-3) | 0.5 | 0.4 | 0.9 | 0.3 | 0.3 | 0.6 |
| SFA | 3.0 | 6.6 | 1.3 | 2.2 | 4.8 | 1.0 |
| Total fatty acids | 20.0 | 32.3 | 4.6 | 14.6 | 23.5 | 3.4 |
| (n-6)/(n-3) | 26.8 | 18.8 | 1.8 | | | |
| LLA/MA | 3986.2 | 50.3 | 88.1 | | | |

November: If the macaques had consumed each group of S + FS + F with Group 2-1-2 leaves

| | g/day | | | E% | | |
|---|---|---|---|---|---|---|
| Fatty acid | (1-1) | (1-2) | (2-1-1 S+FS+F) | (1-1) | (1-2) | (2-1-1 S+FS+F) |
| LA (12:0) | 0 | 0.7 | 0 | 0 | 0.5 | 0 |
| MA (14:0) | 0 | 0.2 | 0 | 0 | 0.1 | 0 |
| MLA (14:1) | 0 | 0 | 0 | 0 | 0 | 0 |
| PA (16:0) | 2.4 | 4.9 | 1.1 | 1.7 | 3.6 | 0.8 |
| PLA (16:1) | 0 | 0.4 | 0 | 0 | 0.3 | 0 |
| SA (18:0) | 0.6 | 0.8 | 0.2 | 0.4 | 0.6 | 0.1 |
| OA (18:1) | 3.7 | 17.3 | 0.9 | 2.7 | 12.6 | 0.7 |
| LLA (18:2n-6) | 12.8 | 7.6 | 1.6 | 9.3 | 5.6 | 1.1 |
| LNA (18:3n-3) | 0.5 | 0.5 | 0.9 | 0.4 | 0.3 | 0.7 |
| SFA | 3.0 | 6.6 | 1.3 | 2.2 | 4.8 | 1.0 |
| Total fatty acids | 20.1 | 32.3 | 4.7 | 14.6 | 23.6 | 3.5 |
| (n-6)/(n-3) | 23.3 | 16.0 | 1.7 | | | |
| LLA/MA | 1839.0 | 49.1 | 73.0 | | | |

February: If the macaques had consumed each group of S + FS + F with Group 2-1-1 leaves

| | g/day | | | E% | | |
|---|---|---|---|---|---|---|
| Fatty acid | (1-1) | (1-2) | (2-1-1 S+FS+F) | (1-1) | (1-2) | (2-1-1 S+FS+F) |
| LA (12:0) | 0 | 0.1 | 0 | 0 | 0.1 | 0 |
| MA (14:0) | 0.1 | 0.1 | 0.1 | 0 | 0.1 | 0 |
| MLA (14:1) | 0.2 | 0.2 | 0.2 | 0.2 | 0.2 | 0.2 |
| PA (16:0) | 1.1 | 1.5 | 0.8 | 0.8 | 1.2 | 0.6 |
| PLA (16:1) | 0.1 | 0.1 | 0.1 | 0 | 0.1 | 0 |
| SA (18:0) | 0.2 | 0.2 | 0.1 | 0.1 | 0.2 | 0.1 |
| OA (18:1) | 0.9 | 3.3 | 0.4 | 0.7 | 2.5 | 0.3 |
| LLA (18:2n-6) | 2.9 | 1.8 | 0.7 | 2.2 | 1.4 | 0.6 |
| LNA (18:3n-3) | 0.7 | 0.7 | 0.8 | 0.6 | 0.5 | 0.6 |
| SFA | 1.3 | 1.9 | 1.0 | 1.0 | 1.5 | 0.7 |
| Total fatty acids | 6.1 | 8.1 | 3.1 | 4.7 | 6.2 | 2.4 |
| (n-6)/(n-3) | 4.0 | 2.5 | 0.9 | | | |
| LLA/MA | 51.9 | 20.7 | 12.3 | | | |

February: If the macaques had consumed each group of S + FS + F with Group 2-1-2 leaves

| | g/day | | | E% | | |
|---|---|---|---|---|---|---|
| Fatty acid | (1-1) | (1-2) | (2-1-1 S+FS+F) | (1-1) | (1-2) | (2-1-1 S+FS+F) |
| LA (12:0) | 0 | 0.1 | 0 | 0 | 0.1 | 0 |
| MA (14:0) | 0.2 | 0.2 | 0.2 | 0.1 | 0.1 | 0.1 |
| MLA (14:1) | 0 | 0 | 0 | 0 | 0 | 0 |
| PA (16:0) | 1.3 | 1.7 | 1.0 | 1.0 | 1.3 | 0.8 |
| PLA (16:1) | 0.1 | 0.2 | 0.1 | 0.1 | 0.1 | 0.1 |
| SA (18:0) | 0.2 | 0.3 | 0.1 | 0.2 | 0.2 | 0.1 |
| OA (18:1) | 0.9 | 3.3 | 0.3 | 0.7 | 2.5 | 0.2 |
| LLA (18:2n-6) | 3.1 | 2.0 | 0.9 | 2.4 | 1.5 | 0.7 |
| LNA (18:3 n-3) | 2.3 | 2.2 | 2.3 | 1.7 | 1.7 | 1.8 |
| SFA | 1.7 | 2.3 | 1.3 | 1.3 | 1.8 | 1.0 |
| Total fatty acids | 8.0 | 10.0 | 5.0 | 6.1 | 7.6 | 3.9 |
| (n-6)/(n-3) | 1.4 | 0.9 | 0.4 | | | |
| LLA/MA | 20.2 | 10.7 | 5.9 | | | |

**Table 14.4** Mean fatty acid content in each group (weight/dry weight %)

| | Leaves and petals | | Seeds, fruits with seeds, and fruits | | |
|---|---|---|---|---|---|
| | 2-1-1 L, P | 2-1-2 | 1-1 | 1-2 | 2-1-1 S + FS + F |
| Soluble part in hexane | 5.0 | 6.4 | 10.4 | 17.6 | 3.2 |
| Yield of fatty acids | 1.4 | 2.3 | 8.2 | 13.3 | 1.9 |
| LA (12:0) | 0 | 0 | 0 | 2.3 | 0.7 |
| MA (14:0) | 2.0 | 3.2 | 0 | 0.5 | 0.3 |
| MLA (14:1) | 1 | 0 | 0 | 0 | 0 |
| PA (16:0) | 28.5 | 20.1 | 11.8 | 14.9 | 23.3 |
| PLA (16:1) | 2.4 | 2.5 | 0.2 | 1.2 | 0.4 |
| SA (18:0) | 3.5 | 2.9 | 2.9 | 2.3 | 3.2 |
| OA (18:1) | 9.5 | 3.4 | 18.7 | 51.5 | 19.4 |
| LLA (18:2) n-6 | 22.8 | 15.3 | 64.2 | 21.9 | 33.3 |
| LNA (18:3) n-3 | 30.7 | 52.8 | 2.2 | 1.1 | 18.0 |

if the same was done for the S + FS + F of group 1-2 in November, the intake of LLA (18:2n-6) was reduced to 5.6E%, while that of C18 monoenoic acid (18:1) was increased fourfold (from 2.7 to 12.6E%). The (n-6)/(n-3) ratio increased to very high values (16.0–26.8) in November because of S + FS + F intake of groups 1-1 and 1-2. However, in February, the macaques consumed many leaves containing a high amount of LNA (18:3n-3), so the ratio of (n-6)/(n-3) decreased to 0.4–4.0, which is nearly the same value as recommended for humans. This (n-6)/(n-3) value would have been considerably lower if they consumed the same amounts of the S + FS + F of the group 2-1-2 in both months (0.4–1.8). Considering physiological functions of eicosanoids produced from PUF, all the groups in February and the group 2-1-1 S + FS + F consumed in November were more nearly ideal than the group 1-1 or group1-2 S + FS + F consumed in November.

Because the (n-6)/(n-3) ratio of the monkey chow was calculated to be 5.1 (Table 14.5), which is nearly the same as the dietary goal in humans, it seems to be appropriate.

Next, we considered the relationships between the low plasma cholesterol level in the Koshima group (measured in February) and their fatty acid intake. We examined whether the Koshima group had consumed less SFA and had a higher LLA (18:2n-6)/MA (14:0) ratio than the bred macaques. In the monkey chow, SFA made up 4.9E%, and the LLA/MA ratio was calculated as 5.8 (Table 14.5). The plasma cholesterol level was thought to begin to increase around this ratio. The intake of 4.8E% SFA was higher than the dietary goal value (4.5E%) in humans and almost the same as that in the monkey chow in the case of group 1-2 S + FS + F intake in November, but in the other cases it was low (0.7–2.2E%). Furthermore, the ratio of LLA (18:2n-6)/MA (14:0) was calculated as 49.1–3986.2 in all cases in November and more than 20 in the cases involving group 2-1-1 leaves combined with group 1-1 or group 1-2 S + FS + F, and group 2-1-2 leaves combined with group 1-1 S + F in February. In contrast, if the macaques had consumed the group 2-1-2 leaves and the group 1-2 or group 2-1-1 S + FS + F in February, the ratio would have decreased to 10.7 and 5.9, respectively, which would have slightly increased their

**Table 14.5** Fatty acid content of monkey chow AS

| | g/dry weight 100 g | E% |
|---|---|---|
| LA (12:0) | 0 | 0 |
| MA (14:0) | 0.49 | 1.1 |
| MLA (14:1) | 0.74 | 1.6 |
| PA (16:0) | 1.35 | 3.0 |
| PLA (16:1) | 0.75 | 1.7 |
| SA (18:0) | 0.39 | 0.9 |
| OA (18:1) | 2.14 | 4.7 |
| LLA (18:2) | 2.85 | 6.3 |
| LNA (18:3) | 0.56 | 1.2 |
| SFA | 2.23 | 4.9 |
| Total fatty acids | 9.27 | 20.4 |
| (n-6)/(n-3) | 5.1 | |
| LLA/MA | 5.8 | |

The water and energy contents of monkey chow AS were reported to be 8.2% and 376 kcal/100 g, respectively, by Oriental Kobo Co. Ltd.; this means that 100 g dry weight contains 409 kcal. The energy percentage of each fatty acid was calculated using this value

plasma cholesterol level. Because of the very low estimated content of SFA (except in group1-2 S + FS + F in November) and the higher ratio of LLA/MA in the plants consumed by the Koshima group compared with the monkey chow, the plasma cholesterol level of the Koshima group might have been lower than that of the bred macaques. As cholesterol is an important material for the plasma membrane, bile acid, and steroid hormones, too low a value increases the rate of mortality and injury reoccurrence.

*Tenebrio molitor* was found to contain a high amount of fat (see Table 14.2). PA (16:0) showed the highest amount of all SFA, as in plants; the contents of OA (18:1) and LLA (18:2n-6) were similar to those in the group 1-2 S + FS + F; and the (n-6)/(n-3) ratio was 21.7 in the larva and 34.3 in the imago. Thus, in summer when they consume a large amount of insects, the (n-6)/(n-3) ratio of the macaques will increase considerably. LLA/MA was 8.2 in larva and 11.4 in imago. As these values are lower than 20 but not lower than that in the monkey chow, the intake of insects will slightly increase the plasma cholesterol level of the macaques.

As Japanese macaques inhabiting cool-temperate deciduous forest subsist on winter buds and barks in winter (Wada and Ichiki 1980; Nakagawa 1997a; Nakayama et al. 1999; see also Chaps. 4 and 5), these items must be analyzed. However, from this study, the following was concluded. (1) Japanese macaques in warm-temperate evergreen forests may be able to consume enough total fatty acids and SFA according to the recommended values for humans when they eat all S + FS + F from group 1-1 or group 1-2 in November. (2) If macaques eat a large amount of S + FS + F (group 1-1 or 1-2), the (n-6)/(n-3) of their diet will increase to the same level as that of a Western meal, which may cause inflammation, thrombosis, and allergic reactions. (3) A low blood cholesterol level is induced by the lower SFA and higher LLA/MA values seen in the diet of wild macaques compared with those observed in monkey chow. (4) High amounts of LNA (18:3n-3) in young leaves may aid the development of the brains of neonates in spring.

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# Topic 3: Toward Understanding the Role of Diet in Host–Parasite Interactions: The Case for Japanese Macaques

**Andrew J.J. MacIntosh and Michael A. Huffman**

## 15.1 Introduction

Central to understanding animal ecology are interactions between consumers and the consumed, whether predator–prey, herbivore–plant, or mycophage–mushroom. A wealth of information exists describing just such relationships (Stephens and Krebs 1986; Stephens et al. 2007). The first systematic and naturalistic study of primates (*Alouatta palliata*: Carpenter 1934) reported a partial list of items consumed by howler monkeys. Since then, countless food lists have been compiled for all groups of primates (for examples, see Richard 1985, table 5.1, pp 164–165). For example, we now have a detailed picture of the diversity of items consumed by Japanese macaques (*Macaca fuscata*) across Japan, from the southern limit of their range on Yakushima Island (Maruhashi 1980; Agetsuma 1995a,b; Hill 1997; Yumoto et al. 1998; Domingo-Roura and Yamagiwa 1999; Hanya et al. 2003; Hanya 2004; Tarnaud and Yamagiwa 2008; MacIntosh, unpublished data) through their northern limit on the Shimokita Peninsula (Izawa and Nishida 1963; Suzuki 1965; Nakagawa et al. 1996; Nakayama and Matsuoka 1998; Nakayama et al. 1999; see also Chap. 5). Although such lists are important, taken alone they are uninformative from a bioenergetics perspective (Nakagawa et al. 1996). Although complementary work examining the nutritional and energetic qualities of food items with respect to metabolic requirements has been and is being undertaken in Japan (Iwamoto 1974, 1982, 1988; Nakagawa 1989a,b, 1997a; Yokota 1989; Soumah and Yokota 1991; Nakayama et al. 1999; Wakibara et al. 2001; Hanya et al. 2007; Tsuji et al. 2008; see also Chaps. 5 and 14), primate nutritional ecology remains in its infancy (Robbins and Hohmann 2006).

Meeting metabolic requirements is far from simple for dietary generalists such as primates, not the least of considerations being that plants produce a variety of chemical compounds (plant secondary metabolites or PSMs) in defense of

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herbivory (Freeland and Janzen 1974; Rosenthal and Janzen 1979; Rosenthal and Berenbaum 1992). PSMs are produced as a result of adaptations by plants that, among other things, can (1) protect plants against the physical environment (e.g., UV radiation); (2) lead to mutualistic relationships between plants and the pollinating insects that have counter-evolved resistance to certain chemicals (i.e., host specificity); and (3) reduce the damage incurred by generalist herbivores (Rhoades 1979). Many examples exist in which mammals, often lacking specific mechanisms for detoxifying certain PSMs, simply avoid eating the plants that contain them (Freeland and Janzen 1974). However, a growing body of evidence highlights exceptions to this rule in nature. In a seminal paper, Janzen (1978) introduced the hypothesis that animals ingest certain PSMs for their chemical, that is, antiparasitic properties. Such chemotherapy now falls within the rubric of animal self-medication, with a poignant example seen in the interactions between chimpanzees (*Pan troglodytes schweinfurthii*) and the medicinal plant *Vernonia amygdalina*, which exhibits antiparasitic properties in vitro (Huffman 1997, 2006; Huffman and Seifu 1989; Huffman et al. 1993; Jisaka et al. 1993; Koshimizu et al. 1994; Ohigashi et al. 1994) and is widely used by humans across Africa for the treatment of various parasitic infections. Studies advocating the hypothesis that animals ingest PSMs for the treatment or prevention of disease are increasingly common (Villalba and Provenza 2007).

Parasites are ubiquitous in nature, and their impact ranges from the benign to the severely pathological, in some cases being a significant driver of host population dynamics (Wobeser 2007). To counteract such organisms, vertebrates have evolved both physiological, that is, the immune system, and behavioral counter-strategies (Hart 1990). Behavioral counter-strategies include the avoidance of disease transmission (Freeland 1980; Hausfater and Meade 1982; Lozano 1991; Gilbert 1997; Hutchings et al. 2001), sickness behaviors associated with the febrile response (Hart 1988), and self-medication. Theoretically, the ingestion of PSMs can be preventative (i.e., medicinal foods) or therapeutic (linked to proximate physiological cues) (Lozano 1991, 1998; Huffman 1997, 2006; Hutchings et al. 2003, 2006). An in-depth description of these aspects is beyond the scope of this chapter, but it is important to understand that although the evolutionary principles behind each are the same, assuming that fitness advantages are conferred to consumers of PSMs through a reduction in parasitism, the behavioral manifestations of these phenomena differ (Hart 2005). There is likely a continuum between medicinal foods—which may be incorporated into an animal's regular diet and likely vary seasonally with infection levels—and therapeutic self-medication, which should coincide with acute disease and involve only rarely consumed items (Huffman 1997). A few studies have attempted to identify potential medicinal foods in the diets of wild primates, including chimpanzees (Krief et al. 2006; Pebsworth et al. 2006), gorillas (*Gorilla* spp.: Cousins and Huffman 2002), and lemurs (*Eulemur fulvus*: Negre et al. 2006).

Despite the abundance of information addressing *what* Japanese macaques eat and *where* they eat it, and to a lesser extent *why* they eat it in relationship to nutritional and energetic requirements, no studies have yet addressed the possibility that the antiparasitic or other medicinal properties of certain PSMs pose another potential selection criterion for consumption in this species. One possible exception is a study by Wakibara et al. (2001) at Arashiyama, which suggests that geophagy, a hypothesized self-medicative behavior (Krishnamani and Mahaney 2000), may allay symptoms of gastrointestinal upset. There is also some evidence that macaques might swallow the blades of Chinese silver grass (*Miscanthus sinensis*: Poaceae) in an effort to control nematode parasitism (Dagg 2009) through a behavioral analogue of "leaf-swallowing" observed in chimpanzees (Huffman and Caton 2001). In any case, to address this gap in our knowledge, we focus here on the potential tri-trophic interaction between diet and parasitic infection to (1) highlight potentially antiparasitic items in the diet of Japanese macaques, (2) establish such interactions within the context of feeding (trophic) ecology, and (3) create a framework for future research in this species. We examine dietary reports from ten populations of macaques across Japan in relationship to known antiparasitic properties of ingested plant items, and create a database from which to build and test hypotheses concerning self-medication in Japanese macaques.

## 15.2 Methods

### *15.2.1 Diversity in the Diet of Japanese Macaques*

To assess the dietary breadth of Japanese macaques, we examined the literature with the criterion that, for any given population, the consumption of at least 50 plant items must be reported to warrant inclusion in our database, regardless of the total number of studies available. Ten populations met this criterion, from a total of 34 source publications, and are included in our analysis (Fig. 15.1). At many of these sites, at least some groups of macaques are provisioned. We show the distribution of wild, provisioned but free-ranging, and captive populations from which the feeding lists were compiled. Discrepancies in the number and nature of studies from which we created the dietary database may have led to variations in the level of completeness of the dietary lists across populations. However, we accept this as inherent in meta-analytical studies of this nature, and believe that our compiled lists are adequately representative of the dietary breadth of the populations under examination.

### *15.2.2 Antiparasitic Items in the Diet of Japanese Macaques*

We constructed a database from the aforementioned sources to guide a two-tiered literature search in our investigation of potentially antiparasitic plant items in the diet of Japanese macaques. First, we examined a subset of the

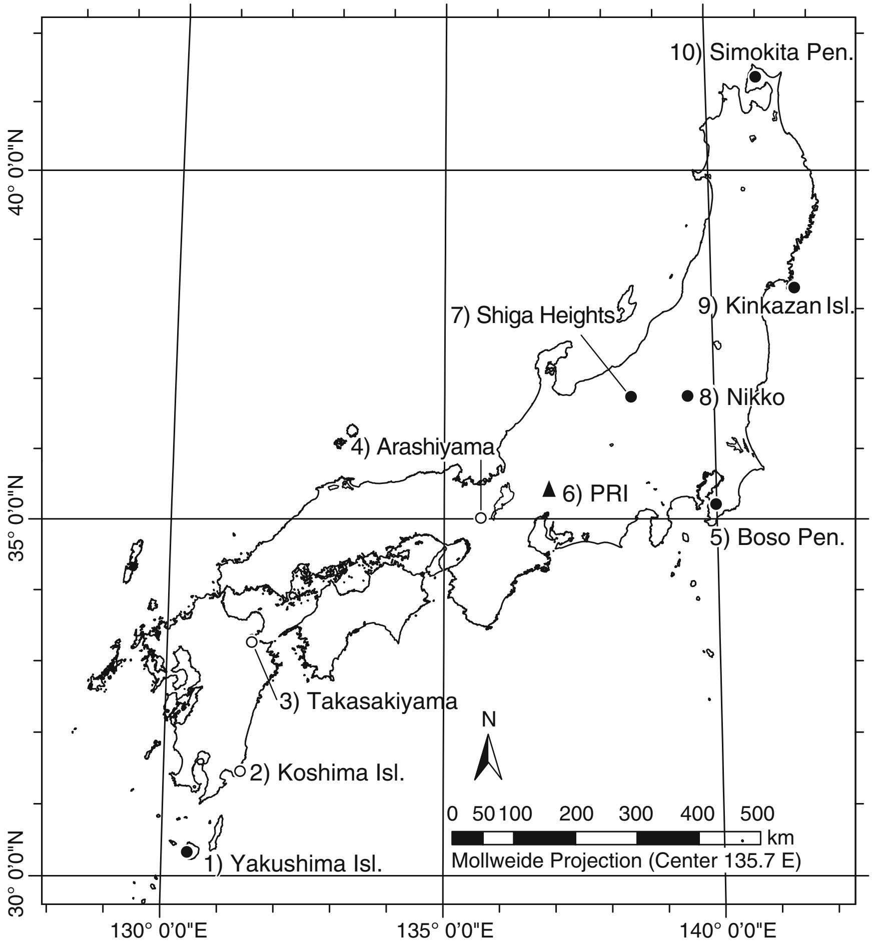

**Fig. 15.1** Populations of Japanese macaques across the Japanese archipelago for which food lists of greater than 50 plant items are available. (1) Yakushima Island (Maruhashi 1980; Agetsuma 1995a,b; Hill 1997; Yumoto et al. 1998; Domingo-Roura and Yamagiwa 1999; Hanya et al. 2003; Hanya 2004; Tarnaud and Yamagiwa 2008; MacIntosh, unpublished); (2) Koshima Islet (Suzuki 1965; Iwamoto 1974; Kimura 1988; Nakagawa et al. 1996; Go 2010); (3) Takasakiyama (Itani 1956; Suzuki 1965; Yokota 1989; Nakagawa et al. 1996); (4) Arashiyama (Huffman 1984); (5) Boso Peninsula (Anonymous 1974); (6) Primate Research Institute (Jaman et al. 2010); (7) Shiga Heights (Suzuki 1965; Wada and Ichiki 1980; Wada and Tokida 1981); (8) Nikko (Koganezawa 1983); (9) Kinkazan Island (Izawa and Nishida 1963; Suzuki 1965; Nakagawa 1989a,b, 1997a,b; Nakagawa et al. 1996); (10) Shimokita Peninsula (Izawa and Nishida 1963; Suzuki 1965; Nakagawa et al. 1996; Nakayama and Matsuoka 1998; Nakayama et al. 1999). Markers: *circles*, provisioned but free-ranging; *filled circles*, wild; *filled triangles*, captive. (The base map is originated from "Boundary data of cities, towns and villages of Japan ver. 6.2" by ESRI Japan Corporation, with permission)

ethnomedicinal literature, i.e., *materia medica*, focusing on medicinal plants used by humans primarily in traditional Chinese medicine (TCM) and its progeny, kanpo, in Japan (Duke and Ayensu 1985; Kimura and Kimura 1991; Yen

1992; Ou 1999). We also consulted an online database of medicinal plants, which cites a variety of ethnomedicinal publications as sources of information (Plants for a Future 1996–2008). Second, we searched the *ISI Web of Science* using the plant species name as a search term to find evidence corroborating the antiparasitic activity of these ethnomedicinal plant items within the scientific literature. In a small minority of cases, studies existed in the Web of Science literature but not in our ethnomedicinal sources.

Because we are concerned here with the interaction between host diet and parasitic infection, we report only those items characterized by antiparasitic properties (anthelmintic, anti-protozoan, antibacterial, antiviral, antifungal, and exhibit activity against external parasites). We also include into this classification those items used in ethnomedicine to treat gastrointestinal symptoms commonly related to parasitic infection (e.g., dysentery). As the concentration of PSMs can vary significantly between different parts of the same plant (McKey 1974), we report bioactive properties at the level of the plant part (item), and thus only cases in which macaques feed on the item in question are included in our analysis. We present descriptive statistics describing the distribution of plant items consumed by Japanese macaques, which exhibit the foregoing properties. Because our study is exploratory by nature, it was not feasible to collect all plant items and systematically screen them for antiparasitic activity. It is also unlikely that all these plant items have received equal attention by pharmacologists and ethnopharmacologists, making it possible that we have underestimated the proportion of potential antiparasitic items in the macaque diet. However, by maximizing the number and types of databases used to assess bioactivity of these plant items, we are confident that for the purpose of this analysis, the method employed provided the best estimates currently available. Furthermore, given that the diet data set was compiled from multiple sites and multiple researchers, it was not possible to assess the relative contribution to the diet of the identified antiparasitic plant items, nor could we examine in detail the availability of such items to each population. These considerations will need to be incorporated into future studies examining the relative importance of antiparasitic items in the macaque diet.

### 15.2.3 Intestinal Parasites of Japanese Macaques

Japanese macaques are infected by a number of intestinal parasites, including five or six species of nematode (*Streptopharagus pigmentatus*, *Oesophagostomum aculeatum*, *Trichuris trichiura*, *Strongyloides fulleborni*: Tanaka and Nigi 1967; Itoh et al. 1988; Gotoh 2000; *Gongylonema pulchrum*, *Gongylonema macrogubernaculum*: Uni et al. 1994) (Fig. 15.2), a cestode (*Bertiella studeri*: Ando et al. 1994), and at least five protozoans (*Balantidium coli*, *Entamoeba* spp.: Hasegawa, personal communication; *Entamoeba dispar*: Rivera and Kanbara 1999; *Entamoeba nuttalli*: Tachibana et al. 2009; *Giardia intestinalis*: Itagaki et al. 2005). An extensive list of parasites infecting Japanese macaques across the country has been compiled from some of

**Fig. 15.2** An infective stage ($L_3$) juvenile nematode of the species *Strongyloides fuelleborni*, cultured from the feces of *Macaca fuscata yakui*. Eggs of this parasite are shed with host feces into the environment, where they hatch and the juvenile worms develop into infective stages before reinfecting new macaque hosts either orally or by penetrating their skin. (Photograph by A. MacIntosh. ×20)

these studies and can be found at http://mammalparasites.org/ (Nunn and Altizer 2005). Gotoh (2000) found a negative relationship between latitude and the diversity of nematode species, that is, species richness, infecting Japanese macaques, and only the Yakushima population was infected by all five species: *G. pulchrum* was found only in this population. However, there is a report that *Gongylonema* spp. may also exist in southern Kyushu (Uni et al 1994).

At present, we know little regarding the effects of nematodiases on the health and behavior of wild Japanese macaques. A recent observation highlights the potential impact of high parasite load on the health and possibly death of a very old female macaque necropsied in Yakushima in the winter of 2007, although the main cause of death was attributed to respiratory infection (Hayakawa et al., under review). If items are selected on the basis of their antiparasitic properties, as we propose here, then greater levels of parasitism should create stronger pressures to select such items. We have restricted our analysis of parasitic challenge to nematode species richness because equivalent data for cross-population comparison of other Japanese macaque parasites do not exist. However, we do not restrict our analysis of antiparasitic items to those that are anthelmintic (i.e., nematocidal), because in many cases, plant chemicals toxic to one parasitic organism can be toxic to others as well, but explicit tests of this are often not represented in the literature. Lacking such tests, then, we assume that all antiparasitic items in the diet at least have the potential to interact with nematode parasites. Thus, we employed a one-tailed Pearson product moment correlation test predicting a negative relationship between the proportion of antiparasitic items in the diet of each population and (1) latitude and (2) nematode species richness. We performed a similar analysis using the proportion of dietary items that are listed in the medicinal plant literature but are unrelated to parasite activity (e.g., antioxidants, stimulants). We make no predictions about the expected relationship between the proportions of these items in the macaque diet and either nematode species richness or latitude, and thus each of these tests is two-tailed. The group at the Primate Research Institute (PRI), Kyoto University, was omitted from these analyses as it is a captive group, albeit kept in an outdoor, forested environment.

A number of studies have described nematode infection in Japanese macaques (Tanaka and Nigi 1967; Kagei and Hasegawa 1974; Nigi et al. 1975; Machida et al. 1978; Horii et al 1982; Itoh et al 1988; Uni et al 1994; Kobayashi et al. 1999), and Gotoh (2000) presents an excellent interpopulation comparison. Many of these studies provided us with the nematode species richness data used in our analyses (see Table 15.1). However, because the majority of these studies were cross-sectional in nature, and many parasites exhibit seasonal patterns (Altizer 2006), including nematodes infecting Japanese macaques in Koshima Islet (Horii et al. 1982) and Yakushima (Dagg 2009; MacIntosh et al., under review), it is possible that species richness may have been underestimated in some populations. Still, multiple studies examining macaque parasites exist for most populations across Japan, and we are thus reasonably confident in the use of these data in our present analysis.

**Table 15.1** Nematode parasites infecting Japanese macaques across Japan

| Population | Nematode species |
|---|---|
| Yakushima Island | *Streptopharagus pigmentatus*[a,c], *Oesophagostomum aculeatum*[a,c], *Strongyloides fuelleborni*[a,c], *Trichuris trichiura*[a,c], *Gongylonema pulchrum*[a,f], *G. macrogubernaculum*[f,*] |
| Koshima Islet | *S. pigmentatus*[a,b], *O. aculeatum*[a,b], *S. fuelleborni*[a,b], *T. trichiura*[a,b] |
| Takasakiyama | *S. pigmentatus*[c,d,e], *O. aculeatum*[c,d,e], *S. fuelleborni*[c,d,e], *T. trichiura*[c,d,e] |
| Arashiyama | *S. pigmentatus*[a,c,e], *O. aculeatum*[c,e], *S. fuelleborni*[a,c,e], *T. trichiura*[a,c,e] |
| Boso Peninsula | *O. aculeatum*[a], *S. fuelleborni*[a], *T. trichiura*[a] |
| Shiga Heights | *T. trichiura*[a,c] |
| Nikko | *T. trichiura*[a] |
| Kinkazan Island | *O. aculeatum*[a], *S. fuelleborni*[a], *T. trichiura*[a] |
| Shimokita Peninsula | *S. fuelleborni*[a,c], *T. trichiura*[a,c] |

*Not included in the analysis because animals were examined after being transferred to the Japan Monkey Centre in Inuyama, Japan

[a] Gotoh (2000)

[b] Horii et al. (1982)

[c] Itoh et al. (1988) and references therein

[d] Kagei and Hasegawa (1974)

[e] Tanaka and Nigi (1967)

[f] Uni et al. (1994)

## 15.3 Results

Japanese macaques from the ten populations examined consume a total of 1,664 plant part items (range, 56–408) from 694 species of 159 families. Of ingested items, 198 from 135 species are known to exhibit antiparasitic properties (Table 15.2). The proportion of these antiparasitic items ranged from 12% to 18% across populations, with a mean ± SD of 0.14 ± 0.02. A further 167 plant items from 133 species exhibit medicinal properties *not* related to parasitic infection, or related gastrointestinal symptoms (mean ± SD, 0.11 ± 0.02; range, 0.06–0.14). Antiparasitic items ingested by Japanese macaques are listed in Table 15.3. One hundred and nine (55.3%) of these 198 items are reportedly used ethnomedicinally by humans to treat gastrointestinal symptoms related to parasitic infection (GI), 45 (22.8%) are antibacterial (AB), 44 (22.3%) are anthelmintic (AH), 36 (18.3%) are antiviral (AV), 27 (13.2%) display activity against external parasites (XP), 15 (7.6%) are antifungal (AF), and 14 (7.1%) are anti-protozoan (AP) (e.g., antimalarial). These properties are not mutually exclusive, as there is considerable overlap in activity among plant items of the same species. A given item can, for example, be concurrently anthelmintic and anti-protozoan, both of which make it more likely to be effective in the treatment of parasite-related symptoms as well.

At the population level, the study group housed in a forested enclosure at the PRI in Inuyama consumed the highest proportion of antiparasitic plant items, followed by groups at Takasakiyama and Arashiyama (Fig. 15.3). Because nematode species richness is negatively associated with latitude among Japanese macaques (Gotoh 2000), we predicted that the proportion of antiparasitic items in their diets would follow the same pattern. We found a tendency for the proportion of such items to decrease with increasing latitude (Fig. 15.4; $r = -0.572$, $n = 9$, $P = 0.054$, one-tailed test), and a strong positive relationship between the proportion of antiparasitic

**Table 15.2** Antiparasitic and other medicinal plant items in the diet of Japanese macaques

| Macaque population | Antiparasitic properties | No known medicinal properties | Other medicinal properties | Total |
|---|---|---|---|---|
| Yakushima Island | 50 (14.9%) | 253 (75.5%) | 32 (9.6%) | 335 |
| Koshima Islet | 29 (15.4%) | 140 (74.5%) | 19 (10.1%) | 188 |
| Takasakiyama | 43 (16.7%) | 181 (70.4%) | 33 (12.8%) | 257 |
| Arashiyama | 16 (15.8%) | 71 (70.3%) | 14 (13.9%) | 101 |
| Boso Peninsula | 52 (13.9%) | 277 (74.3%) | 44 (11.8%) | 373 |
| Shiga Heights | 40 (12.4%) | 245 (75.9%) | 38 (11.8%) | 323 |
| Nikko | 19 (12.4%) | 125 (81.7%) | 9 (5.9%) | 153 |
| Kinkazan Island | 40 (15.7%) | 187 (73.3%) | 28 (11.0%) | 255 |
| Shimokita Peninsula | 49 (12.0%) | 312 (76.5%) | 47 (11.5%) | 408 |
| PRI | 10 (17.9%) | 42 (75.0%) | 4 (7.1%) | 56 |
| Japan | 198 (11.9%) | 1,299 (78.1%) | 167 (10.0%) | 1,664 |

**Table 15.3** Antiparasitic plant items in the diet of Japanese macaques from ten populations

| Family | Plant species | Plant item[a] | Macaque population[b] | Antiparasitic activity[c] |
|---|---|---|---|---|
| Alliaceae | *Allium macrostemon* | BB, L | 3, 10 | XP |
| | *Allium schoenoprasum* | L | 10 | GI |
| | *Allium victorialis* | BB | 10 | AH, XP |
| Anacardiaceae | *Rhus javanica* | B, F, S, SP | 7 | AH, AP, GI |
| | *Rhus succedanea** | F, L, S | 1, 2 | AB, AV, GI |
| Apiaceae | *Glehnia littoralis* | R | 1 | AB |
| Aquifoliaceae | *Ilex integra* | F | 1 | AB, AF |
| Araceae | *Pinellia ternata* | ST | 9 | GI |
| Araliaceae | *Aralia cordata* | P, ST | 7, 8, 10 | AB, AV |
| | *Aralia elata** | B, L | 1, 2, 4, 7, 9, 10 | AV, GI |
| | *Kalopanax pictus* | B | 7, 10 | AF |
| | *Kalopanax septemlobus* | B | 10 | AF |
| Aspidiaceae | *Dryopteris crassirhizoma* | ST | 7 | AH |
| Asteraceae | *Taraxacum officinale* | L | 10 | AB, GI |
| Berberidacea | *Berberis thunbergii** | B, L | 9, 10 | AB, AF, AH |
| | *Epimedium koreanum* | L | 10 | AB |
| | *Nandina domestica* | L | 4 | AV |
| Capparidaceae | *Crataeva religiosa* | L | 1 | GI |
| Caprifoliaceae | *Lonicera japonica* | BD, ST | 3, 9 | AB, GI |
| | *Sambucus racemosa* | F | 7 | GI |
| | *Viburnum dilatatum* | B, F, L | 7, 9, 10 | AH |
| Caryophyllaceae | *Stellaria media* | L, PT, ST | 3, 9, 10 | GI |
| Celastraceae | *Euonymus sieboldianus** | B | 7, 10 | AH |
| Chloranthaceae | *Chloranthus glaber** | ST | 1 | AB |
| Compositae | *Artemisia montana* | L, S | 8 | AP, GI |
| | *Artemisia princeps** | L, PT | 3, 5, 7, 8, 10 | AP, XP, GI |
| | *Bidens biternata* | L | 1 | GI |
| | *Chrisanthemum ornatum** | ST | 1 | AB |
| | *Crepidiastrum lancoleatum** | L | 1 | AP |
| | *Sonchus brachyotus** | L | 10 | AF, GI |
| | *Sonchus oleraceus** | ST | 3, 10 | GI |
| | *Syneilesis palmata** | L, PD, ST | 5, 7, 8, 10 | AV |
| | *Taraxacum officinale* | L | 3, 10 | AB, GI |
| Cornaceae | *Cornus kousa** | F, L | 1, 5, 7, 8, 9, 10 | AB, AP,AV |
| | *Cornus macrophylla* | B | 9 | GI |
| Cruciferae | *Nasturtium officinale* | L | 8 | GI |
| Cucurubitaceae | *Gynostemma pentaphyllum* | L | 10 | GI |
| | *Trichosanthes cucumeroides* | S | 3 | AH |
| | *Trichosanthes Kirilowii* | F | 7, 10 | AB, GI |

(continued)

**Table 15.3** (continued)

| Family | Plant species | Plant item[a] | Macaque population[b] | Antiparasitic activity[c] |
|---|---|---|---|---|
| Cupressaceae | *Chamaecyparis obtusa* | L | 5, 10 | AB |
| | *Juniperus rigida* | L | 5 | GI |
| Dioscoreaceae | *Dioscorea japonica* | BB, R | 3, 5, 10 | GI |
| Ebenaceae | *Diospyros kaki* | F, L | 3, 4, 5, 8, 9 | AB, AH, GI |
| Elaeagnaceae | *Elaeagnus pungens* | L | 2, 3, 4 | GI |
| Ericaceae | *Lyonia ovalifolia* | L | 4, 5 | XP |
| Euphorbiaceae | *Mallotus japonicus** | B, F | 1, 2, 3, 5, 6 | AV, GI |
| Eupteleaceae | *Euptelea polyandra** | L | 5 | GI |
| Fagaceae | *Quercus acutissima* | S | 7, 9 | GI |
| Geraniaceae | *Geranium thunbergii** | L | 10 | AB |
| Graminae | *Phyllostachys nigra* | SH | 3 | GI |
| Grossulariaceae | *Ribes ova-crispa* | F | 10 | GI |
| Illiciaceae | *Illicium religiosum* | F, L | 3, 5 | AB, GI |
| Juglandaceae | *Juglans ailanthifolia* | B | 8 | AH |
| | *Juglans mandschurica* | B | 7 | AB, GI |
| Labiate | *Perilla frutescens* | L, S | 9 | AB, GI |
| Lamiaceae | *Lamium album* | ST | 3 | GI |
| Lauraceae | *Cinnamomum camphora** | B, L, S | 1, 2, 3, 5, 6 | AF, AH, XP, GI |
| | *Litsea japonica** | L | 2 | XP |
| | *Machilus japonica** | L | 2, 3, 5 | XP |
| | *Machilus thunbergii** | B | 1, 2, 3 | XP |
| | *Neolistea sericea** | L | 1, 3, 4, 5 | XP |
| Leguminosae | *Albizia julibrissin* | B | 2, 3, 5, 7 | AH |
| | *Lotus corniculatus** | L | 9 | AH |
| | *Robinia pseudo-acacia* | B, FL, L | 5, 7, 9, 10 | AV, GI |
| | *Trifolium repens** | L | 3, 7, 8, 9, 10 | AB, AH |
| Magnoliaceae | *Magnolia obovata** | BD, L | 9, 10 | AH, GI |
| Meliaceae | *Melia azedarach** | F, S, ST | 1 | AH, XP, GI |
| Moraceae | *Morus bombycis* | B, L | 5, 7, 8, 10 | AB, GI |
| Myricaceae | *Myrica rubra** | B, F | 1, 2, 4, 5 | AH, AV, XP, GI |
| Myrsinaceae | *Ardisia japonica* | L, S | 5 | AB, AV |
| Oleaceae | *Ligustrum japonicum* | L | 2, 3 | AB, GI |
| | *Ligustrum lucidum* | F, L | 6 | AB, AV, GI |
| Osmundaceae | *Osmunda japonica** | L, PT | 5, 8 | AV |
| Oxalidaceae | *Oxalis corniculata* | L, ST | 9 | XP |
| Papaveraceae | *Macleaya cordata* | L, P, ST | 4, 3, 7 | AF, XP |
| Phytolaccaceae | *Phytolacca americana* | F | 6 | AV, GI |
| Pinaceae | *Abies firma** | L, S | 5, 9 | AB |
| | *Abies Mariesii** | B | 7 | AB |
| | *Pinus densiflora* | SP | 4, 5, 7, 9, 10 | AB, AH, AV |
| | *Pinus thunbergii* | SP | 1, 3, 5, 7, 9 | AH, GI |
| Piperaceae | *Piper kadzura** | L | 1, 2 | XP |
| Pittosporaceae | *Pittosporum tobira** | L | 2, 3, 5 | AF |

(continued)

**Table 15.3** (continued)

| Family | Plant species | Plant item[a] | Macaque population[b] | Antiparasitic activity[c] |
|---|---|---|---|---|
| Podocarpaceae | *Podocarpus macrophyllus* | F | 2, 5 | GI |
| Polygonaceae | *Polygonum chinense* | L | 1, 2 | AH |
| | *Polygonum sachaliense* | R | 10 | GI |
| | *Rumex japonicus** | L, ST | 10 | AB |
| Polypodiaceae | *Pyrrosia lingua* | L | 1 | GI |
| Primulaceae | *Lysimachia clethroides* | L, ST | 5, 8 | GI |
| | *Lysimachia sikokiana** | L | 1 | XP, GI |
| Rosaceae | *Duchesnea indica* | F | 10 | AF |
| | *Eriobotrya japonica* | L | 3 | AB, AV, GI |
| | *Prunus grayana* | F | 5, 7, 8, 10 | GI |
| | *Prunus incisa* | F | 5 | GI |
| | *Prunus jamasakura** | B | 4, 10 | XP |
| | *Prunus lannesiana* | F | 5 | GI |
| | *Prunus Maximowiczii* | F | 7 | GI |
| | *Prunus mume* | F | 3, 8, 9 | AB, AH, GI |
| | *Prunus nipponica* | F | 7 | GI |
| | *Prunus pendula* | F | 8 | GI |
| | *Prunus salicina* | F | 8 | GI |
| | *Prunus Sargentii* | F, L | 1, 6, 7 | GI |
| | *Prunus ssiori* | F | 10 | GI |
| | *Prunus xyedoensis* | F | 9 | GI |
| | *Rosa multiflora* | F, FL | 3, 7, 9, 10 | GI |
| Rubiaceae | *Morinda umbellata** | L | 1 | XP |
| | *Paederia scandens** | L | 1, 5, 9 | AH, AV, GI |
| | *Psychotria serpens** | F, L, ST | 1 | AV |
| Rutaceae | *Citrus natsudaidai* | F | 5 | GI |
| | *Phellodendron amurensis* | B | 7 | GI |
| | *Poncirus trifoliata* | B | 5 | AV |
| | *Zanthoxylum ailanthoides** | B | 1, 10 | AV |
| | *Zanthoxylum piperitum* | F | 9 | AH, GI |
| Saxifragaceae | *Hydrangea chinensis** | L | 1 | AP |
| | *Hydrangea macrophylla* | B, L | 5 | AP |
| Schisandraceae | *Kadsura japonica* | F | 2, 5 | GI |
| Simaroubaceae | *Ailanthus altissima** | B, L | 6 | AH, AP, GI |
| | *Picrasma quassioides* | B | 7 | AB, AH, AV, XP |
| Styracaceae | *Styrax japonica** | L | 1, 4 | AB |
| Symplocaceae | *Symplocos chinensis* | B | 8, 9 | GI |
| | *Symplocos prunifolia* | L | 1 | GI |
| Taxaceae | *Torreya nucifera* | S | 7, 9 | AH |
| Taxodiaceae | *Cryptomeria japonica** | B, L | 3, 4, 5, 7, 10 | AB, AF, AV, XP |

(continued)

**Table 15.3** (continued)

| Family | Plant species | Plant item[a] | Macaque population[b] | Antiparasitic activity[c] |
|---|---|---|---|---|
| Theaceae | *Camellia japonica** | L, S, F, FL | 1, 2, 3, 4, 5, 10 | AB, AF, AH, AV, GI |
| | *Eurya emarginata** | L | 1, 2 | GI |
| | *Ternstroemia japonica* | ST | 2 | AP, GI |
| Ulmaceae | *Celtis sinensis* | B | 3, 5, 9 | GI |
| | *Trema orientalis** | L | 1 | AH |
| | *Ulmus davidiana* | B | 7 | GI |
| Urticaceae | *Boehmeria longispica** | L | 1 | AF |
| | *Boehmeria nipononivea** | L | 5 | AF |
| Valerianaceae | *Patrinia villosa* | ST | 3 | AB |
| Verbenaceae | *Callicarpa japonica** | L, SH | 1, 2, 5, 8, 10 | AB, AV, XP |
| | *Clerodendron trichotomum** | L | 1 | AP, AV |
| Vitaceae | *Ampelopsis brevipedunculata* | L | 2 | AB |
| | *Parthenocissus tricuspidata** | L, ST | 1 | AP |

*Species for which studies of antiparasitic activity appear in the Web of Science database

[a] L, leaf; F, fruit; FL, flower; B, bark; S, seed; ST, stem; PT, petiole; PD, pedicel; SP, sap/resin/gum; BD, bud; SH, shoot; BB, bulb

[b] 1, Yakushima Island; 2, Koshima Islet; 3, Takasakiyama; 4, Arashiyama; 5, Boso Peninsula; 6, PRI; 7, Shiga Heights; 8, Nikko; 9, Kinkazan Island; 10, Shimokita Peninsula

[c] AH, anthelmintic; AP, anti-protozoan; AB, antibacterial; AV, antiviral; AF, antifungal; XP, external parasite; GI, gastrointestinal symptoms

items ingested and nematode species richness (Fig. 15.4; $r = 0.818$, $n = 9$, $P = 0.003$, one-tailed test). The proportion of medicinal items unrelated to parasite activity showed no relationship with either latitude ($r = 0.034$, $n = 9$, $P = 0.93$, n.s., two-tailed test) or with nematode species richness ($r = 0.351$, $n = 9$, $P = 0.354$, n.s., two-tailed test).

## 15.4 Discussion

Japanese macaques consume a number of plant items exhibiting antiparasitic properties (Fig. 15.5). The proportion of these items in relationship to the total number of items ingested ranges from roughly 12% to 18% across populations of macaques, and we observed a tendency for populations to ingest higher proportions of antiparasitic items at decreasing latitudes. Furthermore, populations of macaques infected by a greater diversity of nematode species—our measure of the degree of parasitism across populations—incorporated a higher proportion of antiparasitic items into their diets. This was not the case for the ingestion of medicinal plant items unrelated to

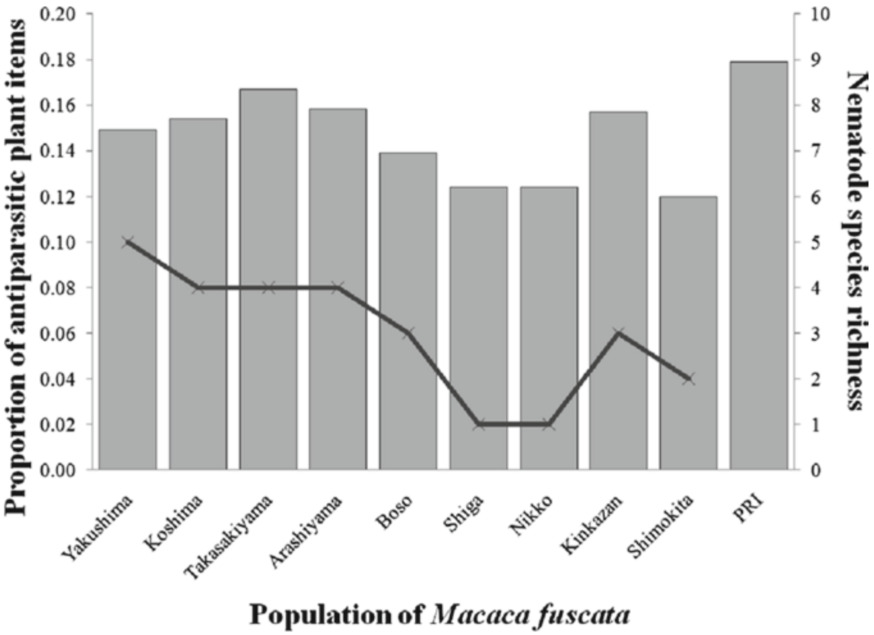

**Fig. 15.3** Proportion of antiparasitic plant items in the diet of Japanese macaques in relationship to nematode species richness. The *y*-axis (*shaded bars*) represents the proportion of antiparasitic items in the diet of *Macaca fuscata*. The *z*-axis (*thick line*) represents the nematode species richness. (Data from sources listed in Sect. 15.2: *Intestinal Parasites of Macaca fuscata.*) Populations are arranged on the *x*-axis in order of increasing latitude [except for the captive group at Primate Research Institute (PRI) shown at *far right*, for which richness data do not currently exist]

parasite activity, which showed no relationship to either latitude or nematode species richness, and this is consistent with our prediction that increased parasitic challenge may coincide with increased ingestion of antiparasitic items. Because parasite species richness is generally lower at higher latitudes (Gotoh 2000; Nunn and Altizer 2006; but see Nunn et al. 2005), these results suggest that variations in the consumption of potentially antiparasitic items across populations of Japanese macaques may in fact be related to relative challenges posed by parasitic infection.

Our focus here is on building a framework for future research rather than on making strong claims about self-medication in this species at this time. Accepting the limitations of the data set (e.g., variability across sites in completeness of dietary databases, identification of antiparasitic plant items; see Sect. 15.2), let us address the possible biological explanations for the observed relationships between antiparasitic items in the macaque diet and both latitude and nematode richness. In general, there is a well-observed trend for biodiversity of many organisms, including plants, primates, and parasites, to increase approaching the equator (Gaston 2000). We have seen that nematode species richness is higher in southern populations of Japanese

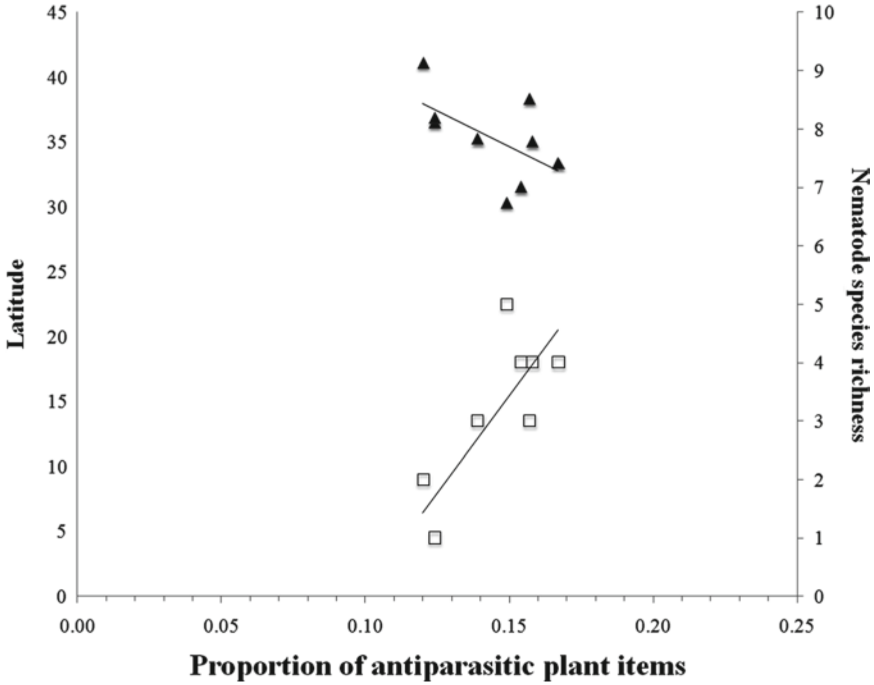

**Fig. 15.4** Proportion of plant items with antiparasitic properties in the diet of Japanese macaques in relationship to latitude (*triangles*) on the *y*-axis, and nematode species richness (*squares*) on the *z*-axis. Latitude: Pearson product moment correlation coefficient: $r = -0.572$, $n = 9$, $P = 0.054$, one-tailed test. Nematode species richness: Pearson product moment correlation coefficient: $r = 0.818$, $n = 9$, $P = 0.003$, one-tailed test

macaques (Gotoh 2000). Among East Asian forest ecosystems, including those within Japan, tree species richness increases with average temperature and thus decreases with latitude (Takyu et al. 2005). Macaques living in the subtropical coastal forests of Yakushima may have access to a greater diversity of food sources than those living in the cooler temperate forests of Shimokita, for example. Interestingly, PSMs such as alkaloids (Levin 1976) and tannins (Coley and Aide 1991) are both more common among plants at lower latitudes, presumably because of greater herbivore pressures (Gauld et al. 1992). This observation seems to leave us with two options: macaques at lower latitudes either consume more potentially antiparasitic plant items spuriously, because PSMs are simply more prevalent in their environment, or because the physiological pressures to do so are stronger, that is, parasitic stress is greater. In fact, the higher prevalence of PSMs at lower latitudes may *force* macaques to consume a wider array of items for reasons of low tolerances for high concentrations of PSMs (Freeland and Janzen 1974). However, we found no relationship between latitude and the proportion of other medicinal

**Fig. 15.5** Japanese macaques on the Island of Yakushima (*Macaca fuscata yakui*). (**a**) An adult female and juvenile feed on the young pinecones of Japanese black pine, known as "kuromatsu" in Japan (*Pinus thunbergii*: Pinaceae). Turpentine contained in the resin of kuromatsu has been used herbally to treat intestinal worms, as well as respiratory diseases such as the common cold, flu, and tuberculosis. (Photograph by Y. Agetsuma.) (**b**) An adult female macaque feeds on fallen fruit and seeds of the wax tree, known in Japan as "hazenoki" (*Rhus succedanea*: Anacardiaceae). Hazenoki seeds have been shown experimentally to inhibit the activity of *Mycobacterium tuberculosis*, as well as both the hepatitis B and HIV viruses. (Photograph by A. Jacobs)

items unrelated to parasite activity. This finding provides evidence that PSMs in general may be available to all populations, but southern populations, or those with greater parasitic challenges, may selectively ingest items that specifically have antiparasitic potential. This realization highlights the need to further explore the relationships between host diet and parasitic infection across populations.

The macaque population inhabiting Kinkazan Island ingests antiparasitic items in roughly similar proportions to populations in the south (i.e., Takasakiyama and Koshima), despite its northern location (see Fig. 15.1). This ingestion is important because these macaques are infected by at least three nematode species, which is more than any of the other northerly populations. What is presumably more important than latitude, per se, to both nematode and plant species richness, is the prevailing climatic condition. The mean annual temperature on Kinkazan is roughly 11°C, but because of its oceanic climate, snow rarely falls in winter months (Nakagawa 1989b). In contrast, although Shimokita, Nikko, and Shiga Heights all have similar or slightly lower mean annual temperatures (between roughly 7° and 10°C, compared to about 20°C in Yakushima: Maruhashi 1980), winter months are often characterized by heavy snow cover (Izawa and Nishida 1963; Suzuki 1965). Such conditions are generally unfavorable for the transmission of macroparasites such as nematodes, with developmental stages occurring outside of their hosts (Nunn and Altizer 2006), and this may lead to lower species richness and a potentially reduced parasitic challenge to the macaques in these areas. Notably, the trophically transmitted nematode *Streptopharagus pigmentatus* (Spiruroidea) has not been observed in any of the northern populations of macaques (Shiga Heights, Nikko, Kinkazan, and Shimokita: Nigi et al. 1975; Nigi 1983, cited in Itoh et al. 1988; Gotoh 2000), although it is one of the most prevalent species infecting macaques in Yakushima (Hernandez et al. 2009) and other southern populations (Kagei and Hasegawa 1974; Horii et al. 1982; Gotoh 2000). This parasite requires a coprophagous beetle (e.g., *Onthophagus* or *Geotrupes* spp.) to complete its life cycle (Machida et al. 1978), and as climatic conditions affect the distribution of many organisms, the absence of intermediate hosts would preclude the establishment of populations of such parasites in their natural definitive hosts, although it must be noted again that at present we do not know to what extent *S. pigmentatus* or any of the other nematode species affects Japanese macaques, at either the individual or the population levels.

The idea that animals respond to physiological stressors by altering their behavior is not new, nor is feeding behavior exempt from this process (see Sect. 15.1). Such behaviors are, as are physiological processes, aimed at maintaining homeostasis, which is negatively affected by parasitic infection (Villalba and Provenza 2007; Forbey et al. 2009). Chimpanzees exhibit two conspicuous, self-medicative behaviors: bitter-pith chewing (Huffman and Seifu 1989; Huffman et al. 1993), which involves PSMs, and leaf swallowing (Huffman et al. 1996; Huffman and Caton 2001), which does not. That these behaviors occur seasonally with increases in nematode parasitism, and in most cases are performed only by observably *sick* individuals, suggests that they are mechanisms to mitigate physiological challenges. Experimental studies have also shown that herbivores can respond to such challenges. Sheep selectively consumed polyethylene glycol when given high concentrations of tannins in their food (Provenza et al. 2000). Lambs were also able to learn to consume compounds that counteracted the effects of previously consumed, illness-inducing substances (Villalba et al. 2006). Insects have also been shown experimentally to self-medicate, specifically when challenged with parasitic infection (Bernays and Singer 2005; Singer et al. 2009). These experimental studies were able to establish cause and effect, which is a considerably more difficult prospect under naturalistic conditions (Huffman and Seifu 1989; Lozano 1998; Hutchings et al. 2003). However, they have also established that animals are capable of recognizing and responding to physiological challenges by selectively consuming appropriate, counteractive compounds.

This point is where traditional studies of feeding and nutritional ecology, which themselves examine ways in which animals maintain homeostasis (Villalba and Provenza 2007), meet the tri-trophic interactions we are discussing here. Studies of Japanese macaques have highlighted their many diet-related adaptations to physiological challenges, such as bark-eating during winter in snow-covered areas (Izawa and Nishida 1963; Suzuki 1965), storing fat for reproductive efforts (Muroyama et al. 2006), and selecting leaves with high protein to fiber ratios but low tannin content in high-altitude areas where fruit, which is eaten in abundance at lower altitudes, is scarce (Hanya et al. 2007; see also Chaps. 4 and 5). We argue that by including an examination of the interactions between primates, plants, and parasites, we may gain a richer perspective regarding how macaques cope with these and other physiological challenges. A new body of literature is rapidly growing that advocates the use of a geometric framework to investigate how herbivores balance their ingestion of both primary and secondary metabolites in similar ways, and with the same functional goal: homeostasis (Villalba and Provenza 2007; Raubenheimer and Simpson 2009). Through such management of "dosage," herbivores can maintain a therapeutic level of PSMs in their systems, incur few costs related to toxicity, and reduce the potentially deleterious effects of parasitic infection (Forbey et al. 2009).

In this chapter, we employed a new approach to increase our understanding of the possible role of diet in host–parasite interactions, using as our model Japanese macaques and their nematode parasites. While pioneering studies of feeding ecology sought to identify important resources supporting primate populations, we argue that these studies remain incomplete until we incorporate into our models the selection of bioactive PSMs, which should also be viewed as important resources for the sustainability of viable populations. We hope that the ideas presented here will stimulate future research in this area and add to our understanding of animal feeding ecology from a holistic perspective. Although much is known about the behavior of foraging in macaques and other primate taxa, and studies in nutritional ecology are becoming progressively more sophisticated through advances in theory, technology, and methodology, researchers must also be aware that PSMs may also represent a selection criterion in complement to or even independent of nutritional characteristics.

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# Topic 4: Did a Habitat Bottleneck Exist in the Recent History of Japanese Macaques?

**David S. Sprague and Nobusuke Iwasaki**

## 16.1 Introduction

Human subsistence activities have affected the global environment ever since humans emerged as a species (Goudie 2005). Hunting, pastoralism, and agriculture, in all their varied forms, have shaped habitats for many nonhuman primate populations around the world. This general principle has been long recognized by primatologists, who have speculated about how human alterations of nonhuman primate habitats affected the distribution or even evolution of monkeys and apes (e.g., Richard et al. 1989; Cowlishaw and Dunbar 2000). The principle applies most clearly where nonhuman primate habitats extend over the regions in the world with extremely long histories of intensive human occupation, especially India and East Asia, where some of the largest human populations in the world have lived for millennia. Especially in these regions, conservation ecology and human ecology are two sides of the same coin. The survival or demise of nonhuman primate populations cannot be explained without an understanding of how people expanded and intensified their subsistence activities.

Japan is an East Asian nation where the nonhuman primate population has survived. Populations of the Japanese macaque (*Macaca fuscata*), although at highly variable densities and degrees of fragmentation (Mito and Watanabe 1999; Oi 2004; see also Chap. 7), still live throughout most of the species original range. The most obvious reason for this is that Japan is very mountainous and heavily forested, precluding many land uses that might have completely obliterated macaque habitats. However, these basic facts only provide a broad background to either the human or macaque ecology of Japan. To judge whether the macaques had ever been endangered, and more importantly now, whether they might be endangered in the

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future, requires an understanding of the history of how the Japanese people have utilized the forests and mountains where macaques were most likely to have found habitats.

Environmental history, as is any history, is full of paradoxical twists and turns that do not allow a straightforward narrative on when or whether Japanese macaques have ever been endangered as a species. Sprague (2002) characterized the conservation status of Japanese macaques today as the best of times and the worst of times. The best of times has come about because the withdrawal of traditional forms of resource utilization has reduced many past threats to macaque survival. The times are worst now because modern forestry has taken over many potential areas of macaque habitats in the form of large conifer plantations, and many macaques are culled in attempts to reduce crop damage to farms inflicted by the macaques. In this paper, however, I take the timeframe back approximately a century, to a time well before the period characterized by Sprague (2002). Traditional natural resources would still have been important, and modern conifer plantations more limited. Was a century ago any better or worse for Japanese macaque?

This paper interprets the literature on the environmental history of Japan to attempt to identify a habitat bottleneck, a time period when macaque habitat may have been at its minimum, over the span of approximately the past 120 years. The paper focuses, in particular, on the degree to which the mountains and hills of Japan were actually forested, and if they were forested, whether those forests were of the kind that would have provided vegetation favored by Japanese macaques. Historians and geographers provide a large literature on Japanese forestry and montane agriculture, some of it in English (Mizoguchi 1996; McKean 1982; Totman 1989; Knight 2003).

The paper draws mainly from three sources. First, I draw on the literature on rural land use under traditional agriculture in Japan. Although little of this literature was written with wildlife in mind, it presents a picture of how Japanese farmers utilized the land around their villages. In particular, there is an important literature on the extent of rural grasslands and land degradation under traditional agriculture in mountainous or hilly regions. Second, I utilize data from a major geographic project led by Himiyama and his colleagues (Himiyama et al. 1995) to reconstruct historical land uses in Japan based on topographical maps. These data allow a geographic comparison between macaque distribution and regional land uses. Third, I focus on one macaque habitat in Chiba Prefecture for which a geographer has provided maps showing relatively precise information about the land uses in the 1890s.

## 16.2 Macaque Distribution in Japan

The Japanese macaque is distributed today on the main islands of Honshu, Shikoku, and Kyushu, as well as the outlying island of Yakushima south of Kyushu. The Ministry of the Environment (MOE), Japan, provides data on the distribution of many Japanese animals as part of the National Survey on the Natural Environment carried out every 5 years on the distribution of the animals and vegetation of Japan. Figure 16.1 uses the data on Japanese macaque presence in the 5×5 km cells from the sixth (2003) national survey. Biogeographically, this distribution corresponds with those of the Japanese mammals that were presumed to have arrived in the Japanese islands via land bridge from the Korean Peninsula and spread to the northern tip of Honshu and the southern tip of the continental shelf in Yakushima (see also Chap. 2).

In theory, at some ancient baseline, macaques may have been distributed throughout the three main islands, Yakushima, and the island of Tanegashima where macaques were last reported in the 1940s (Iwamoto 1995). In historical times, macaques were probably driven out of the plains region and confined largely to the hills and mountains, which still is a large proportion of Japan because mountainous and hilly regions account for about 70% of Japan (Ministry of Internal Affairs and Communications 2009). However, the overall distribution is quite limited compared to the total area of the macaque habitat islands, and macaques are not present in many mountainous areas, implying that Japanese macaque habitats had undergone a bottleneck in the past. Figure 16.1 also shows that many populations are isolated, and various studies on macaque distribution have concluded that macaque populations were isolated and vulnerable to extinction (Oi 2004). By contrast, the MOE concluded that a net increase in macaque distribution has come about between the second and sixth national surveys,

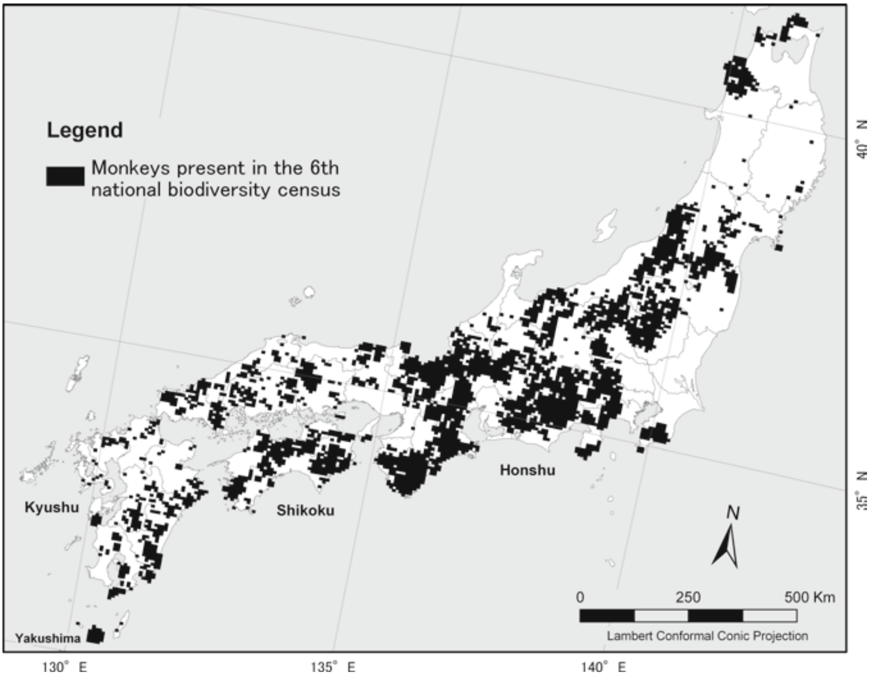

**Fig. 16.1** Macaque distribution in Japan according to the sixth National Survey on the Natural Environment, Ministry of the Environment, Japan

from 18% to 26% of the cells in the macaque habitat islands of Japan (Ministry of the Environment 2004, 2009). The distribution data demonstrate that macaque distribution is very dynamic, with macaque presence expanding in some places while diminishing in others (see Chap. 7).

## 16.3 Natural Resource Utilization in Rural Japan

Astonishing as it may seem to present-day observers, Japan supplied much of its natural resources from domestic sources well into the twentieth century. Many of these resources were obtained from the mountains. Geographers can list a large variety of woodland products that supplied life and industry (Totman 1989; Himiyama et al. 2001). Lumber was, of course, crucial in a nation where even the largest temples and castles were built of wood. Wood was the main fuel in a large variety of industries: steel works for swords and tools, salt production, pottery, and ceramics, as well as charcoal for everyday use. Villages in mountainous regions commonly cultivated swidden fields. Woodlands and grasslands provided green fertilizer, fodder, and thatch, all necessary to sustain agriculture and rural life before the advent of chemical fertilizers, motorized tractors, and roofing. Geographers have estimated the amount of resource area necessary to sustain traditional farming and concluded that many times as much resource area as field area may have been necessary.

The history of natural resource use suggests that the period of most intensive land use in Japan would have been in the nineteenth century, straddling the transition from the early modern period under the rule of the Shoguns, into the modern era after the Meiji Restoration of 1868 when Japan started on the path to industrialization. Some foresters espouse this view, including Ohta (2004), who provides a schematic view of land use change in Japan spanning a millennium, reproduced here as Fig. 16.2. In the figure, “degraded mountain” and “meadow and swidden fields” combine with other land uses to reduce forest area to its minimum amount at about the nineteenth century. Further combined with the effects of woodlands for coppice and lumber, the natural forests had already been reduced to about a third of Japan at that time.

For primatologists, the important question is whether montane land use deprived macaques of usable habitat over long time periods. This is a difficult issue to assess quantitatively because land use was dynamic. A general pattern is that many forest uses left mountains deforested only as part of a cycle of utilization, and forests were allowed to regenerate. Swidden fields and fuel woodlands depend on a forest to regrow. Only a detailed quantitative analysis would do justice to this question of what extent this cyclical forest usage deprived macaques of usable habitat, but few data exist to measure how much and for how long a mountain may have lost vegetation providing food or cover for macaques, and the analysis is not attempted here. Rather, I focus on vegetation that is more clearly disadvantageous for macaques

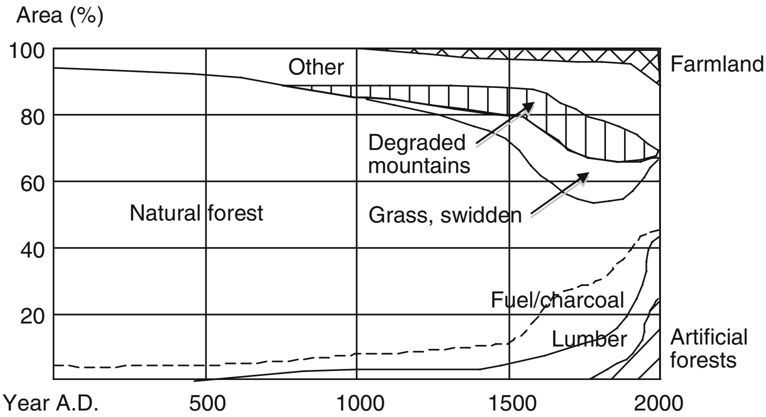

**Fig. 16.2** A model of the forest and mountain land use history of Japan. (Modified from Ohta 2004)

which may have covered large areas of rural and mountainous Japan: grasslands and pine woodlands.

Grasslands are a relatively small part of land use in Japan today. Grassland ecologists today lament that only 1% of Japan is now classified as grassland (*genya*) or meadows and pasture (*saiso-hoboku-chi*) in government statistics on land categories (Ohkubo and Tsuchida 1998). Himiyama et al. (2001) have called the decline in rural grasslands the greatest change in rural land use in Japan over the last century. Rural grasslands are often classified as seminatural grasslands by ecologists because farm communities maintained the grasslands by annual cutting and burning, and these seminatural grasslands were once very common in rural Japan because large grasslands were necessary to supply sufficient amounts of natural resources (Ohkubo and Tsuchida 1998). The actual vegetation within land classified as grassland can range from nearly bare ground to bushland, but the quintessential grass species is *Miscanthus sinensis*, called *susuki* in Japanese. The important point for primatologists is that grasslands, by definition, are treeless, and would provide little food or cover for macaques. Even with a rather broad definition, land described as grassland was highly unlikely to include large numbers of tall, broad-leaved trees, and many grasslands were actually completely treeless.

Pine woodlands were another form of rural land use that was once common in Japan (Fujita 1995; Himiyama et al. 2001). Pine trees (*Pinus densiflora* and *Pinus thunbergii*, *matsu* in Japanese) are very hardy species that can grow quickly in very poor soils. The natural distribution of pines is believed to have been coastlines and mountain crests. Nevertheless, pine woodlands were extremely common in rural Japan until recently because pines could be easily managed for rapid growth and repeated cutting even in poor soils.

From the macaque's point of view, pine is not a preferred food species because Japanese macaques usually eat the fruits or leaves provided by broad-leaved vegetation (Agetsuma and Nakagawa 1998). Occasional records exist of macaques eating parts of pinecones or chewing off the bark of pine trees during winter in cool-temperate forests when there is little food for macaques (Suzuki 1965; Izawa 2004). In this paper, I use pine woodlands as an indicator of forest that is relatively poor habitat for macaques.

## 16.4 Geographic Research on Grasslands in Rural Japan

Ogura (2006) attempted to estimate the grassland area of Japan for a historical period reaching back to the 1880s based on government statistics published by the Ministry of Agriculture, Forestry, and Fisheries and its predecessor institutions. He points out the difficulties of such an estimate because many changes occurred in the words referring to grassland, as well as the definitions and categorizations of various land uses and administrative units of Japan. After accounting for obvious errors, his estimate (shown in Fig. 16.3) suggests the possibility that grassland and bushland had declined rapidly in the late nineteenth century. As the earliest estimate, Ogura calculated that grassland and bushland (*genya*) had occupied 13.2 million hectares at about 1884, a figure that amounts to one-third of Japan's national land area, and about half of total forest-grassland area (*rinya*). By 1900,

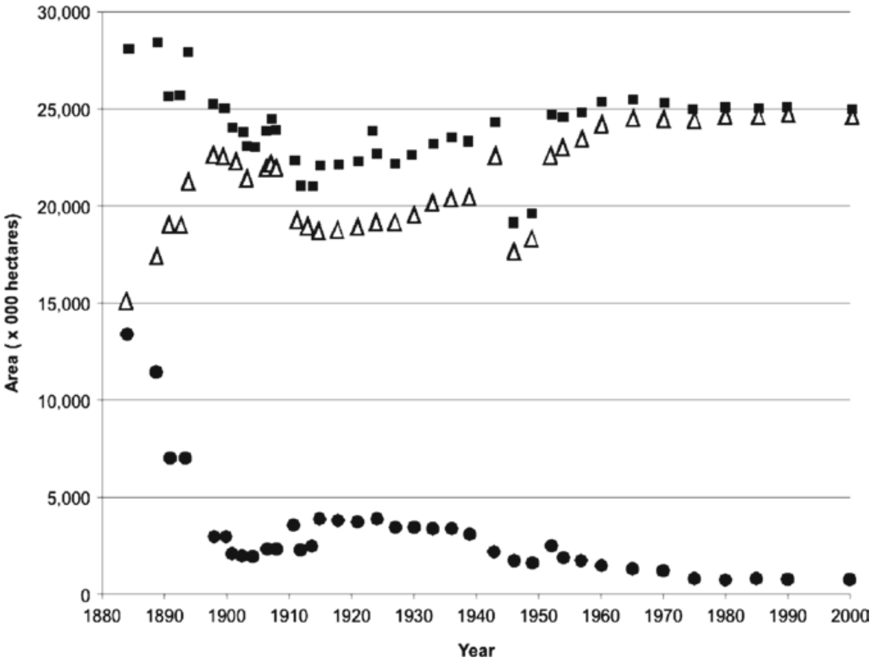

**Fig. 16.3** Estimated historical areas of grassland (*dark circles*), forest (*open triangles*), and their total (*dark squares*) of Japan based on government statistics. (Modified from Ogura 2006)

grassland and bushland had declined to less than 5 million hectares, still a figure much larger than today. Ogura considered these figures to be an overestimate for the period before 1900 and an underestimate after 1900. Nevertheless, he believes that the general picture is accurate, and goes on to suggest that grassland and bushland may have been even larger in earlier periods. He cites official reports prepared by the Lords of several provinces reporting on the natural resources of their domains to the Shogun, in which 50–70% of the "mountains" (*sanya*) are reported to be some type of grassland or bushland. Ogura's (2006) estimate, however, does not allow an assessment of the macaque habitat regions of Japan. He does not provide regional breakdowns, and covers Japan as a whole, including the large, non-habitat island of Hokkaido.

A regional breakdown of grassland area is available in an atlas of environmental history produced by a team of geographers led by Himiyama et al. (1995). The maps of historical land use in the atlas were created from topographic maps, in a massive research project that required Himiyama and his colleagues to read 1,400 topographic maps for multiple time periods and identify the major land use in 2×2 km grids. Figure 16.4 is based on a table from this atlas of land use in each prefecture at about 1900.

Grassland falls under the land use called roughland (*arechi*). This is a cartographic land use category used in Japanese topographic maps designating unfarmed, treeless land without any obvious management regime that includes grassland but not rocky terrain. Himiyama provides data by prefecture on roughland, and forests, with forests broken down into broadleaf, conifer, mixed, and bamboo. In Fig. 16.4 I have shown (a) roughland area and (b) roughland and coniferous forest combined as percentages of the sum of roughland and forest.

By 1900, grassland area may have undergone an initial phase of reduction, assuming Ogura's (2006) estimate is correct, but there was still enough to lead cartographers to mark roughland in many parts of the three major islands of Honshu, Shikoku, and Kyushu where macaques find habitat. In terms of major regions, Kyushu had the largest percentage of roughland, 27.1%, and the Kinki Region had the largest percentage, 31.6%, of conifer. The Chugoku Region had the highest percentage for the sum of roughland and conifer, 52.9%, indicating that a majority of the montane area of this region was poor habitat for macaques. Roughland and conifer show high percentages, especially in the western regions of Japan. At the prefectural level, three prefectures showed more than 30% grassland and seven prefectures more than 60% for combined roughland and conifer. It should also be noted that the remaining forests were not untouched by human activity. Broad-leaved forests were often used as coppice or swidden fields. The Atlas finds that swidden fields could be identified in the topographic maps and maps them scattered throughout the macaque habitat islands.

These data show that in 1900 large parts of Japan's montane areas were either uninhabitable by macaques or relatively poor habitat for macaques. There are two regions, however, that demonstrate important anomalies. The Tohoku Region seems to have had less grassland and more potential habitat for macaques than the rest of Japan, but the present-day distribution of macaques is sparsest in the Tohoku Region,

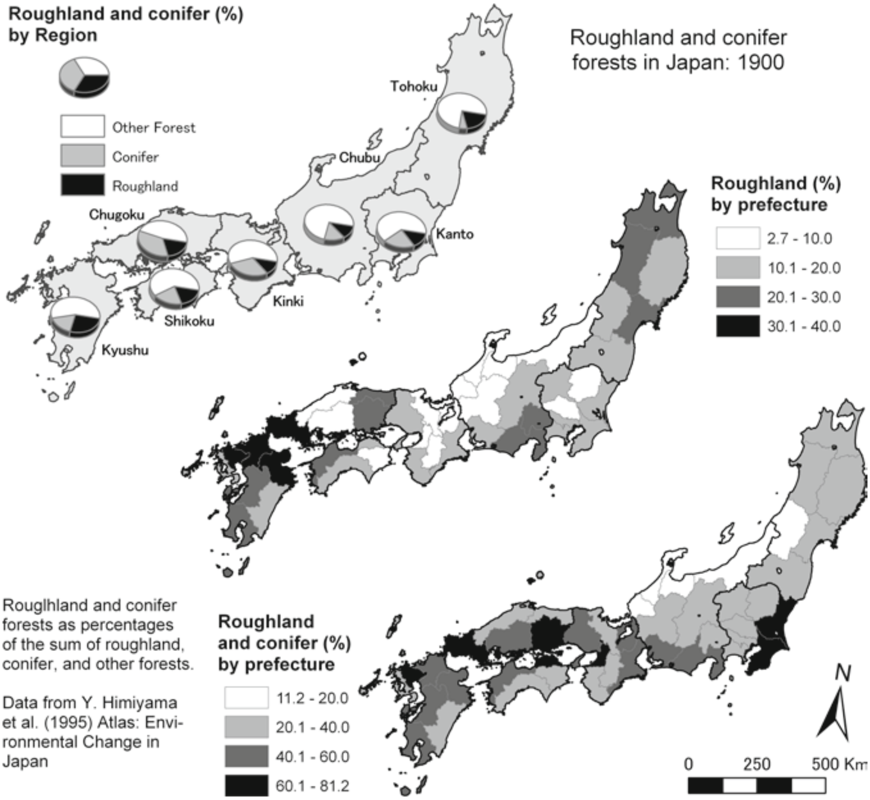

**Fig. 16.4** Roughland and coniferous forest areas of Japan in 1900 by region and prefecture, based on data in Himiyama et al. (1995)

implying that potential habitat does not necessarily translate into survival because of other factors, such as, perhaps, hunting pressure (Mito 1992; see also Chap. 7). In addition, the Kanto Region actually has less potential habitat than implied by its large area because it includes the capital city of Tokyo within the largest plain in Japan. Some of the forests and grasslands of the Kanto were in the plains, far from any macaque populations. Nevertheless, an important macaque habitat is found in one of the prefectures of Kanto with the highest percentage of combined grassland and conifer areas, Chiba Prefecture. Detailed geographic research exists for this habitat revealing the land use context in which this population lived.

## 16.5 The Chiba Prefecture Macaque Habitat

Chiba Prefecture is largely coterminous with the Boso Peninsula. This peninsula has a hilly region midway where an isolated population of macaques has managed to survive. To protect part of the macaque habitat, the national government designated a Natural Monument entitled the Takagoyama Monkey Habitat Area, named after a mountain peak in the center of the monument area. Primatologists have carried out many socioecological studies on the macaques of the Boso Peninsula (e.g., Nishida 1966; Baldwin et al. 1980; Hiraiwa 1981). The Boso macaques had also drawn the attention of conservationists because they nearly went extinct in the early twentieth century (Suzuki 1972).

Geographic research on woodland use reveals that large grasslands and pine woodlands had existed in the Boso Peninsula in and around what is today the macaque habitat. Isogai (1989) published a paper on the distribution of secondary forests in the southern part of the Boso Peninsula based on historical maps. The maps were some of the first topographic maps surveyed in Japan and show land use in the study area at about 1890. The maps distinguish between grassland, pine woodlands, and coppice broad-leaved woodlands; his maps are reproduced here as Fig. 16.5. Isogai's (1989) study area coincides with most of the present-day macaque habitat as reported by the Boso Monkey Management and Research Society (2000).

Within the mapped area as a whole, 21.4% was grassland, 26.8% pine, and 19.0% coppice. Thus, nearly two-thirds of the southern Boso Peninsula depicted in the map area was grassland and pine, providing poor habitat for macaques in the 1890s. Within the macaque habitat region of today, the past land use composition was 25.3% grassland, 17.0% pine, and 39.2% broadleaf. In other words, about 80% of this part of the peninsula, and 60% of the present-day macaque habitat region, was relatively poor macaque habitat.

The larger broadleaf component within the macaque habitat boundaries, compared to the map area, may have contributed to the survival of the macaque populations. Despite the relatively large broadleaf component within the macaque habitat area of the Boso Peninsula, in the early twentieth century, the macaques of this area were confined to two isolated pockets around two mountain peaks (Iwano 1974, 1999). The distribution of macaques has expanded to the extent shown in Fig. 16.5. Whether this macaque population will expand any further is open to debate, and to research, but it is important to remember that the macaques are expanding out into a landscape that is very different from the past, where the grasslands they encounter now are likely to be golf courses.

## 16.6 Discussion

The Boso Peninsula demonstrates that macaque habitats have probably shrunk, expanded, or shifted places many times within the ebb and flow of land uses that swept over the Japanese archipelago. Geographers and anthropologists can help primatologists understand when and how the macaques were threatened by loss of habitat or hunting (Mito 1992; Mito and Watanabe 1999; Knight 2003). This paper focused on the question of when macaques may have suffered a habitat bottleneck, a period when potential macaque habitat was at a minimum, based on historical records of traditional land uses.

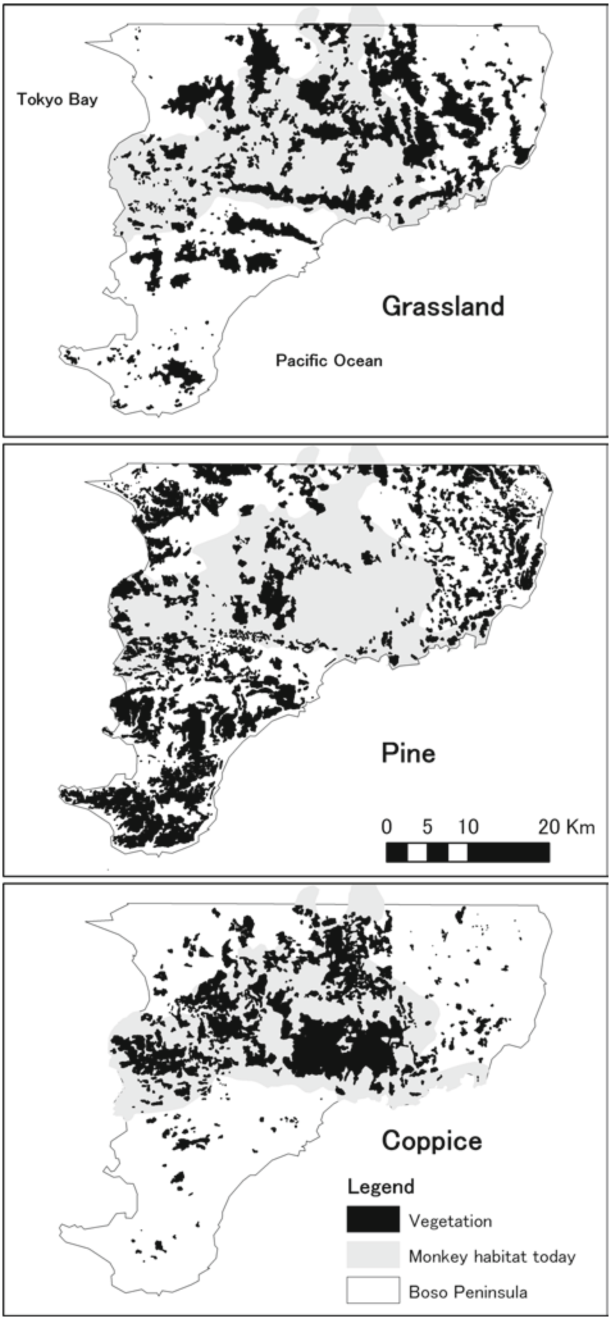

**Fig. 16.5** Grassland, pine forest, and coppice broad-leaved forest areas in the southern Boso Peninsula in the 1890s. (Modified from Isogai 1989)

The general picture of the environmental history of Japan suggests that at least one habitat bottleneck for Japanese macaques may have occurred in the mid-nineteenth century, at a time when Japan obtained all natural resources from domestic sources. In particular, grasslands were an important component of rural and mountain landscapes up into the mid-twentieth century. Grasslands are a useful indicator for assessing the quality of macaque habitats because it is an extreme land use that largely excluded trees. Grasslands were likely to be poor habitat for animals dependent on forests, including Japanese macaques. Historical records are not always clear on the exact extent of grasslands, and the definitions of grassland and bushland have changed over the years, even in government statistics. Nevertheless, these historical records are sufficient to show that grasslands accounted for much larger areas of Japan compared to the present, possibly up to half of the mountainous areas of Japan according to early government statistics, and often more in areas that fell within the purview of the feudal lords who kept records on the natural resources of their domains.

For forested environments, quantitative analyses are necessary to accurately assess their quality as macaque habitat, but few quantitative data exist to allow such an assessment. However, primatologists can make relative, qualitative assessments of whether various types of vegetation can provide habitat for macaques. In general, coniferous trees provide less food for macaques, as macaques eat mainly fruits, berries, acorns, and new leaves of broad-leaved trees (Agetsuma and Nakagawa 1998). Macaques may be able to survive in coniferous forests to the extent that the forests provide cover, or are mixed with broadleaf vegetation or other vegetation providing food (Hanya 2004). However, for forests classified as coniferous on maps, enough of the standing trees should have been conifers for cartographers or foresters to classify them as such. Thus, the areas mapped as coniferous forests probably provided some cover but less food than broad-leaved forests for macaques. Up through the mid-twentieth century, coniferous forests were more likely to have been pine (Fujita 1995).

Broad-leaved forests are more difficult to assess for their quality as macaque habitat. Macaques may be able to survive in broad-leaved forests under heavy human utilization so long as the tree cover remains sufficient in an area to justify its classification as forest. The human presence itself, as swidden farmers, charcoal makers, or hunters, may have some influence on macaque populations, but that is beyond the scope of this paper.

In summary, historical records suggest that Japanese macaques have passed through habitat bottlenecks in the past. Whether Japanese macaques will pass through future habitat bottlenecks depends on the land use regimes of the future. Ironically, Japanese macaques may be experiencing a net gain in total forest cover as a consequence of the end of traditional resource extraction. However, little net change in the overall area of relatively poor habitat may have occurred, assuming that approximately half of Japan's mountains and hills had been grassland or bushland in the past, while today, forestry statistics classify approximately half the forest area in the macaque habitat islands of Japan as artificial forests, which are mostly conifer plantations, largely of cedar, hinoki, or larch (Sprague 2002; see also

Chap. 7). Japanese macaques may suffer a net loss of habitat in the future if the conifer plantations expand further or the remaining broad-leaved forests are subject to logging and heavy utilization, as they had been in the past.

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# Topic 5: Resolution of Human–Macaque Conflicts: Changing from Top-Down to Community-Based Damage Management

**Katsuya Suzuki and Yasuyuki Muroyama**

## 17.1 Introduction

Human–wildlife conflicts have become a major concern in many countries. These conflicts range from wildlife being a nuisance in daily life and crop-raiding, to wildlife being a threat to human life. Such conflicts have been observed in Japan, where the activities of wild mammals such as sika deer (*Cervus nippon*), wild boar (*Sus scrofa*), Japanese black bears (*Ursus thibetanus japonicus*), and Japanese macaques (*Macaca fuscata*) have caused serious damage to agricultural and forestry products, and their activities around human settlements have impacted human life in a variety of ways. The Ministry of Agriculture, Forestry and Fisheries, Japan, reported that total agricultural damage caused by wild mammals was 13.2 billion yen in 2007 (Ministry of Agriculture, Forestry and Fisheries, Japan 2008a). To alleviate these conflicts, researchers have developed theories and techniques of wildlife damage management.

Japanese macaques are one of the major agricultural pests in Japan. Crop damage by macaques occurs in all prefectures of Japan, other than Hokkaido, Okinawa, and Ibaraki where macaques do not occur. Over the past 5 years (2003–2007), macaques have caused approximately 1.5 billion yen of agricultural damage each year, which is the third highest damage level caused by wild mammals in Japan (Ministry of Agriculture, Forestry and Fisheries, Japan 2008b). Japanese macaques are highly social, intelligent animals, and their excellent agility and learning capacity, combined with dietary and behavioral flexibility, appears to make them adaptable and efficient crop-raiders. Consequently, macaques are recognized as the most troublesome crop-raiders by most Japanese farmers.

In addition to the economic damage of commercial harvests, farmers have also suffered social and psychological damage caused by crop loss and the macaques' activities around human settlements. Damage to small-scale farming, for household

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consumption, by macaques could result in a decreased motivation to continue farming in mountainous areas, where the human population has been declining and aging since the 1960s. As macaques habituate to the local people and environment surrounding human settlements, they lose their fear and cautiousness around humans, and often escalate their behavior into threatening people and intruding into houses (Fig. 17.1; see Chap. 7).

To alleviate conflicts between humans and macaques, two different approaches have been adopted in Japan. One is the traditional top-down damage management approach conducted by local government, such as population control and construction of fences. This approach has dominated, but many problems have been experienced with this approach, as described here. The other is the community-based damage management approach, which entails involvement of and positive action by local people, that is, guarding, chasing, fencing, and eliminating attractive foods in and around human settlements. This approach has been gradually spreading in Japan.

In this topic, we describe the top-down damage management approach applied Shimokita Peninsula, Aomori Prefecture, and discuss the problems of this approach, focusing on the involvement of local people in damage management. The community-

**Fig. 17.1** Macaques raiding rice crops

based damage management approach for macaques is then described and its effectiveness, applicability, and prospects discussed. This topic is a summary of several articles published in Japanese (Suzuki 2002, 2005, 2007, 2008).

## 17.2 Crop-Raiding by Japanese Macaques Living in Shimokita

Shimokita Peninsula is located in the north of Honshu Island, the northernmost habitat of nonhuman primates (Fig. 17.2). Macaques have been recorded crop-raiding since the 1960s at Wakinosawa village in the south of the peninsula. Nevertheless, macaques inhabiting the peninsula have been protected by law as a Natural Monument

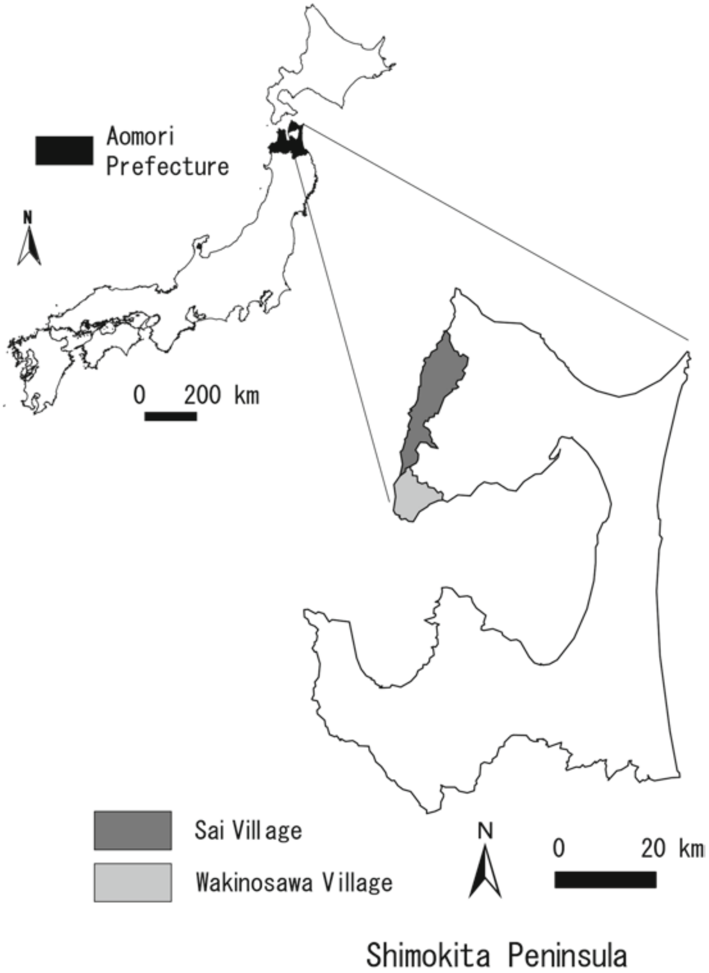

**Fig. 17.2** Sai village is in the northwest of Shimokita Peninsula, Aomori Prefecture, located in the northernmost of Honshu Island

since 1970. In Sai village, located in the north of Shimokita Peninsula, macaques started to cause crop damage in 1991. In 1994, as a main countermeasure against crop-raiding by macaques, local government started a management project to construct electric fences around farmlands using subsidies (Table 17.1). Two types of electric fences, a vertical electric net fence and a wire electric fence, were constructed, and both were expected to be effective against macaques given adequate maintenance. All material and construction costs for the electric fences were paid for by the local government, while farmers were obliged to maintain the fences encircling their farmlands appropriately. However, Suzuki (2002) reported that in 2001 only 23% of these fences had been maintained adequately (Fig. 17.3a–c). Consequently, most of the fences no longer have any effectiveness against macaques.

**Table 17.1** Construction cost and length of electric fences constructed in Sai village each year (Suzuki 2005)

| Year | Project cost (in million yen) | Total length (m) |
|---|---|---|
| 1995 | 2.9 | 460 |
| 1996 | 2.9 | 429 |
| 1997 | 9.1 | 1,340 |
| 1998 | 18.0 | 2,250 |
| 1999 | 18.0 | 2,284 |
| 2000 | 12.0 | 1,240 |
| 2001 | 12.0 | 1,046 |
| 2002 | 12.0 | 1,086 |
| 2003 | 13.1 | 944 |

The local government has spent 1.0 billion yen over 9 years from 1995 to 2003 on construction of electric fences around crop fields, using subsidies

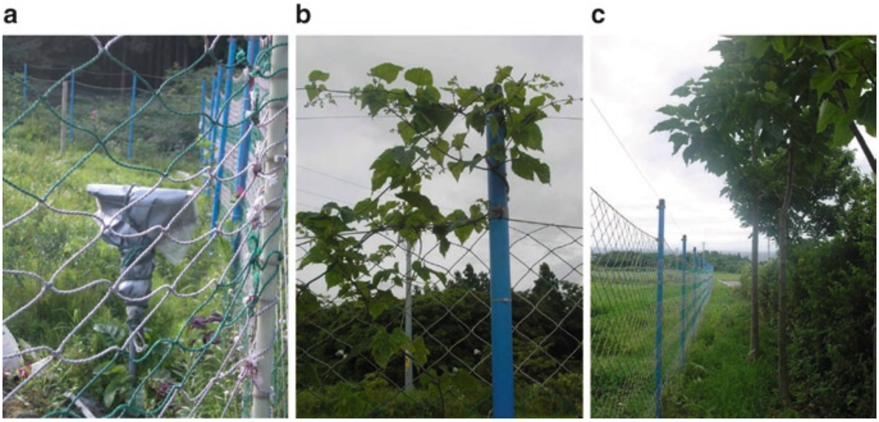

**Fig. 17.3** Examples of poorly maintained electric fences. (**a**) A covered solar panel that does not supply adequate voltage. (**b**) An electric net fence short-circuited by vines winding around the pole and positive electric lines. (**c**) Trees standing close to an electric fence are used as an access route to the cropland

This case illustrates some typical problems relating to human involvement in the top-down damage management approach employed in Japan. In the case of Sai village, various social factors may hamper farmers from engaging cooperative maintenance of the fences.

## 17.3 Insufficient Cooperative Management of Electric Fences by Local People

### *17.3.1 Small-Scale Agriculture in Sai Village and Complex Ownership Patterns for Farmlands*

Agriculture in Sai village is small-scale farming for household consumption involving mostly vegetables. Average farm acreage per farmer was recorded as 37 a in 2005 (Ministry of Agriculture, Forestry and Fisheries, Japan 2008c). Most of the farmers are elderly people. Of 26 electric fences constructed in 2001, only 6 of the fences encircled a single farm and were thus managed by one farmer (Suzuki 2002). The other 20 fences enclosed more than one farm and thus each was managed by two or more farmers. In addition, ownership of farmlands is complicated: some farmers used only their own croplands, but others also used part of another owners' croplands. Relationships between farmers and landowners may also be complex; some farmers are related to landowners, and others are friends or acquaintances. As rent for the cropland, farmers pay something as a token of gratitude, such as a small part of the harvest crop, a year-end gift, or some money, but not a fair rent based on an agreement with the owners. Such complex social relationships among residents in the village characterized by vague relationships between farmers and landowners, as well as small-scale agriculture for home consumption, underlie insufficient cooperative maintenance of the fences.

### *17.3.2 Insufficient Cooperative Maintenance of Electric Fences*

As already described, farmers are obliged to maintain the fences encircling their farmlands appropriately. If a fence encloses more than one farm cultivated by more than one farmer, they must maintain it cooperatively. For electric fences to remain functional, it is necessary to maintain a suitable voltage at all times and to block any openings that could possibly be used by animals. In the case shown in Fig. 17.4, all seven farmers were requested to maintain the fence cooperatively. However, this task ended in failure as it was not done effectively.

There were two reasons why farmers were unable to cooperatively maintain their fences: first, there were individual differences among farmers in knowledge of electric fences, and second there were differences in the willingness and motivation

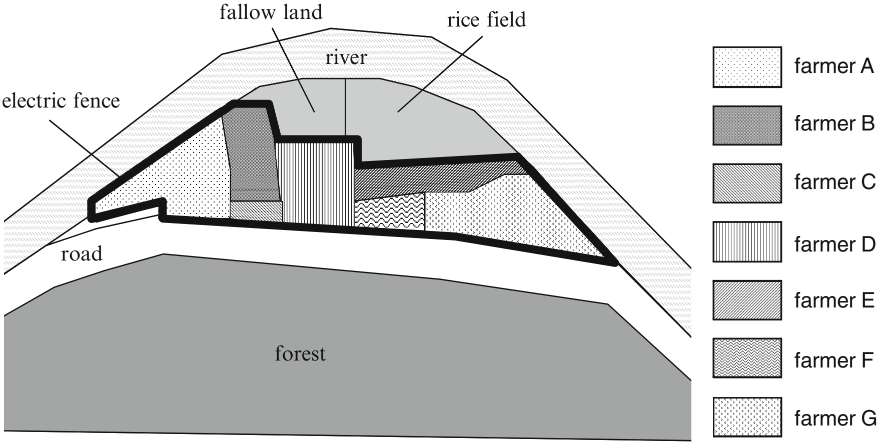

**Fig. 17.4** An example of an electric fence surrounding several croplands. The length of the fence is 463 m, and it encircles seven croplands, cultivated by seven farmers (A–G), whose total area is 4,846 m$^2$. All these croplands adjoin the fence, and each of the seven farmers is obliged to maintain the fence cooperatively

to carry out the maintenance. Maintenance of electric fences needs a certain level of knowledge of the properties of electricity. However, it appears that it is very difficult for all the farmers engaging maintenance to have such knowledge. Willingness or motivation to carry out maintenance of the fences may be facilitated by the actual experience of crop damage by macaques and/or the placement of a high value on harvests. Both these factors may differ significantly among farmers. Farmers cultivating croplands far from forest edges sustain a lower risk of crop damage and may thus feel relatively less incentive to carry out maintenance.

Such individual differences among farmers, in particular the behavior of unmotivated farmers, are recognized as a critical issue by the motivated farmers. Nonetheless, frequently, overt requests for cooperative management of the fences do not occur, as farmers want to avoid destroying or souring their relationships with neighbors and others in the same village. When such a situation continues for a while, then crop-raiding by macaques continues or even escalates. The motivated farmers then start to see their own activity in trying to maintain the fence as useless and insignificant. In this way, originally motivated farmers may become unmotivated and the whole cooperative maintenance system for the fences becomes trapped in a vicious circle.

### *17.3.3 Unsuccessful Elimination of Access Routes Used by Macaques*

Even if farmers maintain the fences adequately, crop-raiding by macaques still occurs if the farmers are unable to effectively eliminate footholds (i.e., trees or buildings close to fences) or to block openings (holes, ditches, etc.) used by animals. Such footholds and openings may remain left as they are, whenever local people base decisions on social, economic, psychological, and institutional factors but not on scientific findings or theories.

The social relationship between a tenant farmer and landowner is one of the most typical factors to hinder the blockage of such access routes. A tree or building close to an electric fence may be used by macaques as a route to cropland (Fig. 17.5), and thus eliminating such a foothold is an important task for the management of the electric fence. However, if the tree or building is owned by the landowner, then the fence management efforts of the tenant farmer may be hindered because the landowner will not remove the tree or building for various reasons.

Figure 17.6 illustrates such a case where macaques frequently use Japanese cedars (*Cryptomeria japonica*) adjoining croplands as access routes to cropland encircled by an electric fence. In this case these trees are planted in the land owned by X. All the farmers Y and Z, and landowner X, recognize the risk that macaques may raid crops by using the trees. Farmer Y appears to have a higher risk of crop-raiding, but is unable to request X to cut down the trees, possibly because he rents a cropland from X for nothing. Landowner X himself has also a risk of raiding of his own crops, but he will not cut down the trees because the following incoherent logic.

"I realize that I should cut down the tree, but I don't do it because I planted the tree as a gift for children and grandchildren. I also hesitate to do it solely for my farming since I don't know how long I can continue farming."

Other landowners may have other reasons to not cut down the tree. For example: that the tree is an owner's memory of childhood, that is, "the tree was planted when I was a child." Another reason is that the tree is a landmark of the border between neighbors. Alternatively, a landowner may wish to let a tree grow until the treetop reaches a high-voltage cable so that the power company will pay compensation for cutting the tree down, even if he realizes that macaques use the tree as a route for raiding.

**Fig. 17.5** A macaque jumping into a cropland from a hut standing close to an electric fence

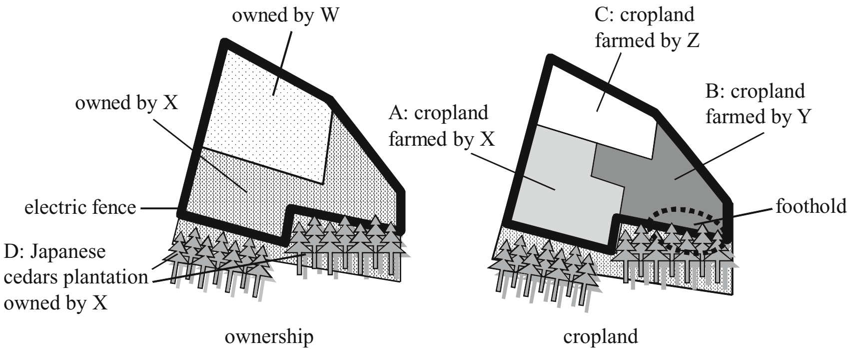

**Fig. 17.6** A case study where macaques frequently use trees (Japanese cedars) adjoining croplands as access routes for crop raiding. Croplands encircled by the electric fence are owned by either W or X, and are farmed by X, Y, and Z. Area A, cropland owned by X and W and farmed by X; area B, cropland owned by X and W and farmed by Y; area C, cropland owned by W and farmed by Z; area D, Japanese cedar plantation, owned by X

As seen in these cases, even if landowners perceive a risk of raiding by macaques to their own crops, they may still not eliminate access routes as a countermeasure. This observation would suggest that farmers will experience many more problems in negotiating such issues with landowners who do not farm. Consequently, footholds and openings used by macaques frequently remain as they are, and many farmers feel discouraged from engaging in appropriate maintenance of the electric fences.

### *17.3.4 Farmers' Perception of Agriculture*

In Sai village, farming is conducted as a low-profit, multipurpose activity. Harvests are used for household consumptions, gifts for relatives and neighbors, and for a small extra income (Figs. 17.7a, 17.8a,b). The purposes of farming are varied and include a means of livelihood, maintaining good health, as a habit or a hobby, and for socializing with neighbors, but do not include large commercial activities (Suzuki 2007; Fig. 17.7b). In such farming, some farmers appear to have relatively little incentive to protect their agricultural products because they value the activity of farming itself rather than the products of farming as important in their daily life. This idea suggests that their perception of farming significantly affects whether or not fences are maintained appropriately (Suzuki 2007).

The traditional top-down approach has provided materials and costs for damage management, but it has paid little attention to the importance of social factors, particularly the issues related to effective damage management, as just described, which encompass a human dimension. The many unsuccessful cases of damage management found all over Japan are a testament to this difficulty.

**Fig. 17.7** Questionnaires investigating the farming practices of local people. (**a**) Use of agricultural products ($n = 182$). (**b**) Purpose of farming (Suzuki 2005)

## 17.4 A Community-Based Damage Management Approach

### *17.4.1 What is the Community-Based Damage Management Approach?*

The major countermeasures to wildlife crop-raiding adopted to date have been top-down damage management approaches of population control and construction of fences, based on biological findings. These traditional top-down approaches have

**Fig. 17.8** (**a**) A farmer, pleased with the harvest for household consumption. (**b**) A farmer carrying harvested potatoes as gifts for relatives living far away. Most farmers recognize farming itself as an important activity in their daily life

not considered issues that have a human dimension and thus have not been developed as appropriate damage management projects encompassing a wide variety of social conditions in different regions.

However, a new methodology for damage management for monkeys that takes into account the human dimension has recently been developed in Japan (Inoue 2002; Muroyama 2003). This approach proposes that it is crucial to manage the behavior and environment of both wildlife and humans to alleviate and control the damage caused by wildlife. That human behavior and perception may unconsciously facilitate crop-raiding by wildlife has been emphasized. In this methodology, damage management explicitly targets local people and farmers, as well as the wildlife and their habitat. In comparison the traditional top-down management approach only targeted the wildlife and habitat. In other words, this approach, called community-based, requires individual involvement of and positive actions by local people for damage management.

This community-based approach involves manipulating the human factors related to the occurrence of crop damage. This concept includes changing people's incentives for damage management, and thus this method may have a wider application for a variety of social situations. One of the most important principles of this approach is to reduce the food resources available to wildlife, such as crops, fruit, garbage, disposed vegetables, unharvested fruit, etc., in and around human settlements (Inoue 2002; Muroyama 2003, 2005). These types of food resources around human settlements are likely to attract wildlife, resulting in increasing crop damage

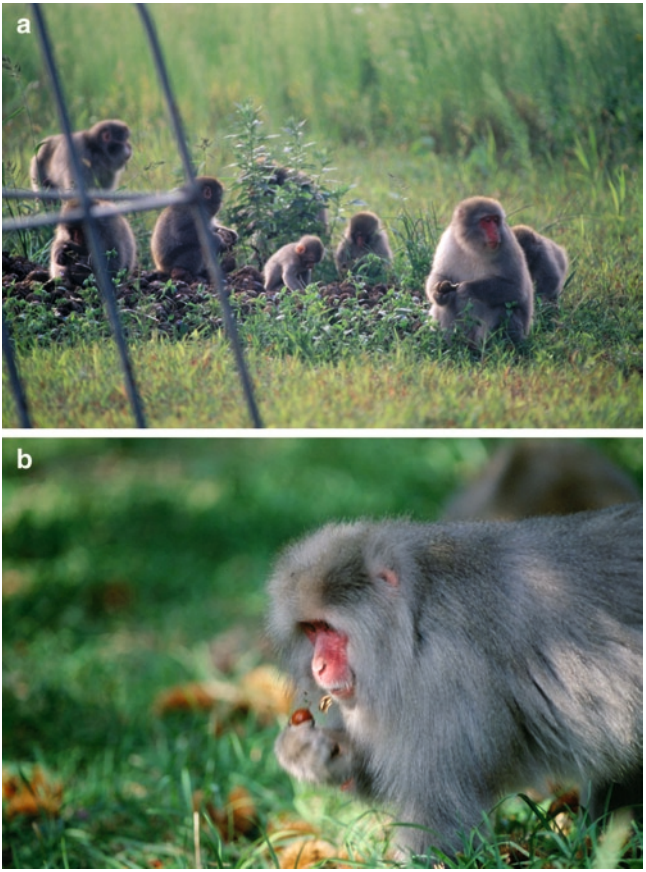

**Fig. 17.9** Macaques feeding on abandoned potatoes in the postharvest season (**a**) and on unharvested chestnuts (**b**)

(Fig. 17.9). Another important principle is to invoke fear and cautiousness of humans and the human-related environment within wildlife by using activities such as chasing or scaring wildlife, such that wildlife feel uncomfortable in and around human settlements (Fig. 17.10).

### 17.4.2 *Promotion of Damage Management Practices by Local People*

To promote community-based damage management effectively, it is crucial that the entire village tackles this issue as a whole and that each farmer manages their cropland appropriately against wildlife. This form of management has been initiated in

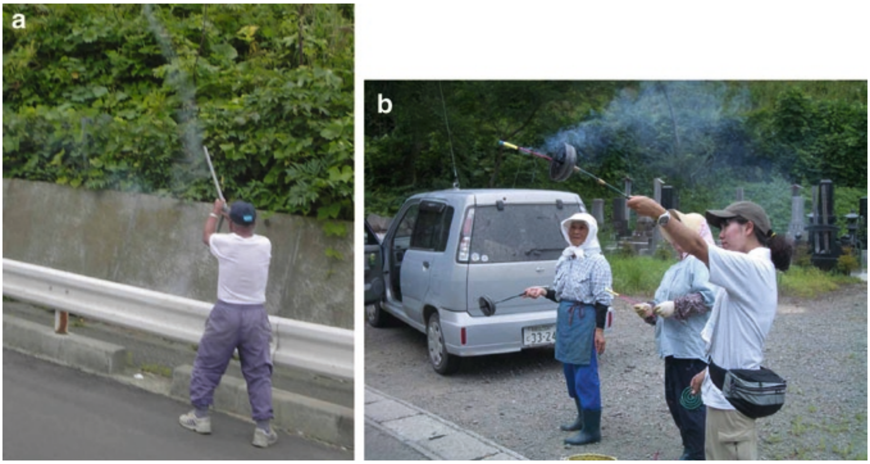

**Fig. 17.10** Residents driving macaques away using fireworks under the guidance of the local government

some prefectures, particularly in prefectures where official agricultural divisions and/or institutions have actively participated in projects, with slogans such as "planning for villages to be undefeated by wildlife damage" or "wildlife damage management by all the villages."

For example, in Totsukawa village, Nara Prefecture, the adequate information and technical support provided by prefectural workers from agricultural divisions has promoted local damage management practices and has successfully reduced crop damage by macaques (Inoue et al. 2004). However, another case suggests that whether the provision of knowledge and techniques for damage management results in more active participation by local people may depend on the social conditions (Suzuki 2002, 2007). Suzuki (2007) stated that it is important to carefully examine what social factors are more likely to increase or decrease the incentive for local people to engage in damage management practices on a case-by-case basis.

Currently, we have limited knowledge of ways in which to encourage damage management activities in local people because of the short history of research in this field. Inoue et al. (2004) suggested that inexpensive and convenient management techniques should be developed according to farming system, farmers' capacity, and social conditions, and then local communities should be familiarized with techniques according to these factors. Other possible factors relating to the farmers' incentive to participate may be the level of knowledge of theory and techniques, the presence of an administrative system or organization to provide support to farmers, the relationships between the administration and farmers, and so on. Introducing a special value to agricultural products may also be an effective way to encourage farmers' participation. In Shiga Prefecture, crops unpalatable to wildlife have been promoted as special indigenous agricultural products (Yamanaka 2009).

### *17.4.3 Complementary Collaboration by Local Government and Local People*

To promote damage management by local people, local government must collaborate with local communities in a complementary manner in management practices. Furthermore, local government and local people must recognize a shared aim to reduce damage caused by wildlife. They must also recognize that to achieve this purpose efficiently each of them must play their role in the damage management process appropriately (Muroyama 2003). For example, population control or the construction of fences in a wide area should be conducted mainly by a local government, while management practices such as fencing croplands, reduction of available foods for wildlife in the village, and chasing wildlife should be undertaken only by the local people. Joint management projects including all these practices are needed to alleviate damage effectively and efficiently.

Within such community-based management, local government still has an important role in providing various supports for the damage management activities of local communities (Fig. 17.10). In locations where local government previously provided top-down damage management, such as population control and the construction of fences over a long time period, the local communities are less likely to take on management activities by themselves and depend on the intervention of local government initiatives for damage management (Nakamura et al. 2007; Suzuki 2008). In such cases, local people have very little knowledge of management techniques to counter crop-raiding by wildlife, and thus provision of information regarding and knowledge of theory and techniques for damage management by holding workshops for villagers and by distributing brochures on damage management are crucial to the effective implementation of such methods. In addition, local government needs to facilitate consensus among villagers on damage management activities.

## 17.5 The Future of Community-Based Management in Japan

In recent years, in Western countries, where wildlife management has a longer history, the concept of wildlife management has turned from biologically based management, conventionally designed by an expert, into community-based management tackling various human–wildlife conflicts in modern society with complex value systems (Decker and Chase 1997). As part of this shift, stakeholder involvement has become a central element of contemporary wildlife management (Chase et al. 2001). Furthermore, co-management, requiring stakeholder involvement at multiple stages of the management process, from the setting of broad policy goals through to evaluation, not just in decision making, is seen as the next step (Chase et al. 2000). These Western community-based management projects focus on stakeholder involvement in the management process.

Community-based damage management in Japan has developed independently of that found in Western communities. In the Japanese approach, the basis of the management method is farming and giving local people adequate knowledge of theory and techniques for damage management in the course of their daily life. Thus, sufficient and effective communication between farmers and authorities to facilitate community-based management should be encouraged.

To develop and extend community-based wildlife management in the future in Japan, it is not only necessary to promote damage management by local people, but also to consider the long-term conservation of local macaque populations as a part of the management project. To achieve this, a wide variety of stakeholders, including researchers, need to be involved in the management process. Continuous effort must be made to build consensus between stakeholders, with the aim of constructing a support system for community-based management within local government.

Although human–wildlife conflicts start with actual damage caused by wildlife such as crop damage, human relationships within the management process may result in more serious social conflicts (Suzuki 2008). For example, relationships between stakeholders with different concepts of value may be a social factor making conflicts more serious. During the process of community-based damage management, an integrative approach to reduce wildlife–human conflicts, not only adjusting interactions among wildlife, habitats and humans, but also mitigating conflicted interactions among humans where wildlife is the reason for the interactions, is necessary (Riley et al. 2003). Whether or not community-based management as described here becomes firmly established in Japan may depend on the development of the human dimension of wildlife management.

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# Topic 6: Social Object Play Among Juvenile Japanese Macaques

**Masaki Shimada**

## 18.1 Introduction: Some of the Substantial Difficulties of Research of "Play"

Many authors have studied juvenile Japanese macaques (*Macaca fuscata*) for investigating various research topics for more than 60 years since Japanese primatologists started provisioning them at many sites, such as Koshima Islet in Miyazaki or Arashiyama in Kyoto. Our accumulated knowledge of Japanese macaques is vast and varied, as this book shows. Few expert primatologists have studied the play behavior of Japanese macaques as a main research topic, with the exception of early studies by Hayaki (1983), Koyama (1985), Imakawa (1990), and my recent study (Shimada 2006). The play of Japanese macaques is a largely unexplored field of research.

Several researchers from various fields have been interdisciplinarily interested in the play of animals (Fagen 1981). These researchers acknowledge the importance of studying play behavior among animals. A famous cultural anthropologist, Johan Huizinga (1955), called humans *Homo ludens* (Man the Player), stating that the play of humans is an essential part of humanity. We can, therefore, expect to develop our knowledge about the origin and evolution of humanity when we study play behavior of nonhuman primates, our close relatives in evolution.

Many ethologists, however, have experienced and noted the many difficulties in studying play behavior of any animal species, including primates (e.g., Fagen 1981; Burghardt 2005). I have discussed and summarized two main reasons why it is difficult for ethologists to study animal play behavior (Shimada 2009).

The first reason is simple but critical for ethological study. Since the sociobiologist Edward O. Wilson complained about the lack of ethological definition of animal play behavior in *Sociobiology* (Wilson 1974), no one has succeeded in proposing a definition of play behavior with which all researchers are satisfied,

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even though several researchers have made efforts to do so (Burghardt 2005). We have no common view on what behavior or which behavioral category should be called “play” thus far, although anyone can easily imagine and perceive the meaning of the word “play,” or “play behavior.”

The second reason is more practical. Many of the modern researchers studying animal behavior tend to design their research plans to reveal a function as an ultimate factor of the behavior they want to investigate. They build hypotheses about the function of the behavior, and then verify these hypotheses. Because many researchers agree to employ one of the criteria of play as behavior, which seems to have no direct function, most researchers who adopt the so-called hypothesis-verify approach inevitably hesitate or avoid studying play behavior.

Although these substantial problems to study animal play behavior are not easy to solve, it is logically possible to avoid approaching such difficulties directly and to research play behavior by finding “detours,” to avoid debate on the definition of “real” play, and not to engage in identifying what the function of play is. The purpose of this paper is to introduce my own research of play behavior of juvenile Japanese macaques from a unique point of view as such a detour (Shimada 2006). For new ethologists, who hope to research primate play behavior, I would like to suggest some interesting phenomena of play among juvenile monkeys correlating with play among human children, and then call their attention to play behavior as a concrete and possible research topic.

Thus, hereafter, I will use the word “play” just for the sake of convenience and will not ask whether what I call “play” can really be defined as play or not. The word “play” in this paper indicates particular kinds of behavioral or interactive patterns, which some ethologists, including myself, agree to call play, but others do not.

## 18.2 “Social Object Play” Among Arashiyama Macaques

Researchers have traditionally divided animal play behavior into the following three categories and have conducted their studies on the structures and functions of each of the three categories: “locomotor play” as solitary activities, such as running, leaping, swimming, or rolling; “object play” as solitary activities holding detached portable objects, including pushing, pulling, or breaking an object; and “social play” as interactions among two or more individuals, such as “play-fighting” or “play-chasing.”

Think of the following three patterns: two domestic dogs play tug-of-war by biting a tree branch and pulling it at both ends. A juvenile macaque runs dragging a tree branch and the other gives chase from behind. Human children play a game of baseball, or chess. All three examples include features of social and object play. We call such a combined category “social object play (SOP).” I broadly interpret the meaning of SOP to make it possible to address the many patterns of SOP observed in nature. For example, in the broadest sense, SOP includes cases in which one of the juveniles holds an object eventually during social play.

In its narrowest sense, it includes games where the objects must be moved according to the strict rules.

Even though SOP has been observed in many animal taxa and varies according to species (Fagen 1981), few studies have examined SOP incorporating characteristics of both categories of social and object play.

Primate researchers must be interested in SOP from the perspective of object possession among monkeys: when a limited valuable object is unclaimed, a dominant individual will most likely have access to it. However, there is also a so-called "prior possession rule" (Bakeman and Brownlee 1982), whereby individuals rarely compete directly for valuable portable objects such as food items that are already claimed by other individuals, even when the object holders are subordinates. If juvenile monkeys automatically and strictly apply this prior possession rule during SOP, nonholders should keep their distance from a possessed object or its holder during play, which means that stealing an object from a holder should be rare, and SOP would not be expected to continue for long periods.

Taking this background into account, let us examine the following description of an interaction observed among juvenile Arashiyama macaques.

Case 1: SOP between two juveniles (May 8, 2000)

Only two juveniles in the same matriline (*Momo*-matriline), whose abbreviations were "*M2*" (*Momo-597898*; 2-year-old female; *M1*'s aunt; dominant) and "*M1*" (*Momo-59789299*; 1-year-old female; *M2*'s nephew; subordinate), continued playing socially from 1300, intermittently, in the woods away from the other group members:

Time 13′20″28. Both of them sat on the ground 3 m away from each other. *M2* found an object in the bush where she sat, and picked it up. The object was a steel semicircular hoop, having a diameter of approximately 30 cm and a width of about 3 cm. *M2* handled the object.
13′20″56. *M1* ran toward *M2*, and *M*2 ran in an attempt to escape with the object. *M1* chased *M2*.
13′21″09. The two animals sat 1 m away from each other.
13′21″30. *M2* ran away from *M1* with the object and *M1* chased *M2*.
13′21″47. *M1* stole the object and escaped immediately from *M2*. Now *M2* chased *M1*.
13′22″09. Both sat 1 m away from each other.
13′22″20. *M2* stole the object and escaped immediately from *M1*.
13′22″30. Both of them grappled with each other on the ground, while *M2* kept holding the object.
13′22″37. *M2* stepped 1 m away from *M1* and sat down.
13′23″04. *M2* dropped the object, picked it up immediately and walked away from *M1*, while *M1* kept sitting without reaction.

From the features such as continuous interaction including play-fighting and play-chasing with an object, we can judge their interaction as SOP.

During this observation period of ≥1.5 min, I noticed several features of the object they held and their interaction. First, the steel hoop was obviously trash

**Fig. 18.1** A scene of "play chasing with a target object" (PCT) among juveniles of Arashiyama. A holder of a maple branch (*left*) escapes from a nonholder (*center*)

discarded by humans, which is inedible to macaques and thus has no value as food. Second, while playing socially with the hoop, they paid no attention to the other objects around them, even though it was easy to find several other kinds of portable objects in the woods, such as twigs. Third, although both of them experienced holding the hoop at least once, the holder was always chased during play-chasing. Fourth, at any given time only one individual held the object: there was never a situation when both of them held the object at the same time, like a tug-of-war. Finally, despite the differences in age and relative rank, both of them stole the object from each other without any agonistic competition over the object.

The features of interactions above can be summarized as follows: (1) multiple individuals use an object as a target of play; (2) the holder of the target escaped from nonholder(s). Hereafter, I define repetitive play-chasing that includes two features above as "play chasing with a target object (PCT)" (Fig. 18.1). PCT is logically a particular interactive pattern observed as a type of SOP, as well as "tug-of-war," or situations where a socially playing individual held two or more objects, or an object holder chases a nonholder, and so on.

These descriptions obviously contradict the prediction above, suggesting that SOP mechanisms differ from those applied in the prior possession rule. Thus, my research was focused on the mechanisms that made interactions such as PCT possible.

## 18.3 Methods

The subjects were all the juveniles (defined as 0- to 4-year-old individuals; $n = 41$) of the provisioned Arashiyama E group (hereafter, "Arashiyama") at Iwatayama Monkey Park in Kyoto Japan, which is open to both researchers and tourists.

All the macaques in Arashiyama have been identified (Koyama et al. 1992). Data collection was conducted in summer of 2000 (38 days; 246.7 h), after I identified every juvenile in the group.

To collect data on continuous interactions occurring around an object, I employed, so to speak, the focal "object" sampling method, which is a modified version of the sequence sampling method and focal animal sampling method (Altmann 1974): When I observed a juvenile holding an object by hand or in the mouth, I began to follow the object and the holder. If the focal object moved to a new holder, I recorded the time and continued following the object and the new holder until the object was finally abandoned. I made a note of the species and kinds of the objects whenever possible.

I successively recorded the name of object holder, the names of other individual(s) within a 3-m radius, and various types of interaction among them. I operationally divided these interactions into nine exclusive categories: (1) play-fighting, (2) play-chasing, (3) tug-of-war, (4) taking an object from a holder, (5) walking together, (6) other active interactions, (7) stopping, (8) clinging, and (9) unknown. I defined a bout of SOP as a continuous series of active interactions (1–6) concerning one focal object with between-play intervals of <1 min. Participants of an SOP bout were defined as individuals who actively interacted in the bout at least once, and a "long" SOP bout was defined as a bout, which continued for ≥0.5 min.

I noted the start of play-chasing between an object holder and nonholder(s). For each of these moments, I recorded the name of the holder and any nonholders within a 3-m radius, along with information about which individuals were chased. I analyzed the relationship between the role of an object holder and a chaser during play-chasing in SOP bouts. Detailed information on methods and definitions is given in Shimada (2006).

## 18.4 Summary of Results

I observed 298 bouts in total. An analysis of SOP revealed the following features: Ninety percent or more of juveniles (37 of 41) participated in SOP at least once during the observational period. Forty-four percent of the bouts that I could observe completely were long SOP bouts, and the longest bout lasted for >15 min. These results suggest that SOP was not a rare activity for most Arashiyama juveniles, and they often continued SOP for long periods.

I identified 135 objects held in long SOP bouts. Juveniles held almost any kind of portable objects that they could access in the environment. A total of 108 natural objects (80%) were held in SOP, consisting mostly of plants ($n = 107$), such as branches, rotting wood, ferns, or herbs, and a stone ($n = 1$). On the other hand, 23 artificial objects were held (17%), such as plastic bottles, or materials made of steel, as in Case 1. However, the juveniles were never observed to hold pieces of wild fruits they could access in the environment or food items such as soybeans or banana provided by the park staff or tourists. Within the range of natural objects, I identified 28 tree species, and all of them (except *Clethra barbinervis*, which was held once) contained some parts that are edible to macaques in Arashiyama, according to lists of the Arashiyama macaques' food (Murata and Hazama 1968; Huffman 1984).

For ≥90% of the duration of SOP, an individual held only one focal object and others within a 3-m radius held no object. In contrast, situations where two or more individuals held the same focal object at the same time, as in a tug-of-war, or an individual held two or more objects, were observed only rarely and did not last for long.

I observed 373 starting moments of play-chasing between an object holder and nonholder(s) in total. In the case of play-chasing, there was a strong tendency for an object holder to assume the role of chasee, independent of the number of nonholders around (Fig. 18.2). In addition, the tendency was revealed to be independent of the relationship of attribution between them, such as sex, age, relative rank, or kinship.

Holder-reversal of a focal object occurred, on average, more than once per long SOP bout which I observed completely; this suggests that holder-reversals happened frequently. In most cases, the new holder assumed the role of chasee, and the former holder chased the new holder or just stopped playing.

Juveniles rarely exhibited serious aggression or submission concerning objects during SOP.

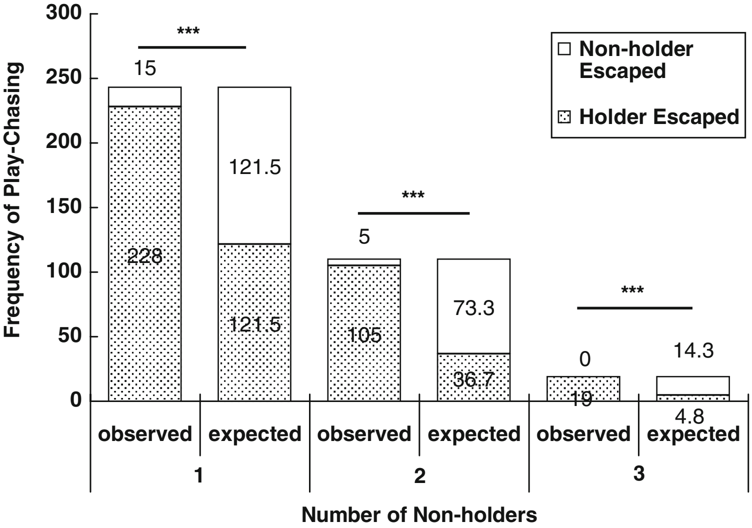

**Fig. 18.2** Frequency of a holder or nonholder escaping in play-chasing during "social object play" (SOP). For this analysis, one case in which the number of nonholders was unknown ($n=1$) was excluded. Each expected frequency was calculated based on the assumption that all participants had an equal chance of being chased. $^{***}P<0.001$ (binominal test). [From Fig. 1 in Shimada (2006), with kind permission of Springer Science+Business Media]

In summary, most SOP among the juveniles of Arashiyama had two regulative interactive features. Multiple juveniles treated only one object as a target of play. The holder of the target escaped from nonholder(s) in play-chasing. As defined, such interactive patterns were considered to be PCT. Although PCT is only one of logically possible and typical play patterns of SOP, it was the most common interactive pattern among juveniles whenever SOP was observed.

## 18.5 Discussion

### *18.5.1 Juveniles' Perception and Continuity of SOP Bout*

Juveniles of Arashiyama held almost any kind of objects they could find in their environment. It is interesting to note that most of the natural plants that the juveniles played with socially contained edible parts. Because they were provisioned with plenty of nutritious food, the macaques seldom or never fed on these wild plants, except for a few kinds of fruits, during the study period. Thus, the values of the objects as food juveniles held in SOP were considered to be very low for Arashiyama juveniles.

Although it was expected that SOP would not continue for long periods if juveniles apply the prior possession rule, the result was the opposite. Perception of the value of the objects as food for Arashiyama juveniles seems to explain the reason why SOP among them could be continuous: even though participants apparently perceived the ownership of the object, they did not seem to respect the possession of object, because they perceived the value of the object as food at the same time. In addition, I never observed juveniles playing socially with any food items provisioned by humans. That is, because the values of the objects as food they held in SOP were low, the prior possession rule rarely operated among juveniles.

### *18.5.2 Comparison Between PCT and Play-Tag*

It is suggested that both the nature of the object and cognition of it by juveniles affected their interaction. As a result, they generated clear interactive regulation among SOP, represented by PCT: an object holder was chased by nonholder(s) in play-chasing, independent of differences in sex, age, relative rank, or matriline. In addition, holder-reversals were frequently observed, and new holders were likely to immediately assume the role of a chasee after the holder-reversal. These results suggest that "being a holder of a target object" was associated with "taking the role of chasee" in play-chasing in a level of the cognition of each juvenile.

When human children are engaged in play-tag, in their cognition, "being named as It ("Oni" in Japanese) by the others" is associated with "taking the role of chaser." This common cognition among playing children makes smooth role-reversal in play-tag possible, in which, if a child who takes the role of It chases and succeeds in touching another, the child who has been touched takes over the role of It.

From the point of view of comparison between play-tag among human children and PCT among juvenile macaques, it is notable that their structures seem to be opposite to each other: in the former, one individual (It) will assume the role of chaser and all the others chasee, while in the latter, one individual (object holder) will assume the role of chasee and all the others chaser. Our observation, however, suggests that juvenile macaques mediated the concrete object instead of words such as "It" or "Oni" and could achieve role-reversals and continuous play-chasing in PCT as children in play-tag.

### *18.5.3 Semantics Among Monkeys?*

Even though the object held in SOP had no value as food and there were several substitutes in the environment, it was the very object held by juveniles at the specific moment, not other similar substitutes, that had a particular value or meaning as a target of SOP for playing juveniles. In addition, as we discussed above, "being a holder of a target object" seemed to be associated with "taking the role of chasee" in SOP.

Researchers in fields of cultural sciences, such as semantics, may consider these phenomena important, because in a lexicon, semantics is the study of meaning: how a sign refers to particular phenomenon. From the semantics point of view, the phenomena can be interpreted in terms of new social value or meaning being generated in playful interactions among juvenile macaques, and the target object worked as a kind of "sign," which referred to the target of play and the chasee as one of the roles in play-chasing.

I often observed that when an object holder accidentally dropped the object, such as a twig from a tree, the holder and the nonholders attempted to pick up the very twig on the ground even though there were several other similar twigs around. Using some ideas of semantics, these observations can be understood as follows: once they regarded the twig as a sign referring to the target, the signification could continue, to some extent, even when no one held the twig.

We humans give social or personal meanings to external phenomena, which are not always derived from their primary meanings. For children who play with a doll house, a handful of plastic beans may be regarded as the dolls' dinner. When we think about semantics, we are likely to consider the human ability to use symbols, such as language, and therefore regard this as a matter of communication of only humans, not of animals. However, the observation of SOP suggests that even Japanese macaques, who never use language, can give a social meaning to a thing in certain situations.

### 18.5.4 Concentration of Interests and Continuous PCT

As shown in case 1, when one of the socially playing juveniles picked up an object, or when a juvenile approached another juvenile who held an object, juveniles eventually concentrated their interests on that particular object, and as a result, an SOP would be started. Even though SOP started with only two juveniles initially, as time passed, other juveniles participated one after another, and, as a result, the SOP bout would continue for a long period.

Figure 18.3 illustrates a concrete example of a long SOP bout (8.48 min) in which many juveniles participated. Throughout the bout, the timing to participate or quit SOP varied among the 11 juveniles. The decision of when to participate or quit SOP seemed to be up to each juvenile, and permission to do so was not required from the others. For example, some juveniles, such as *Ko9398*, held the cup and participated continuously, whereas others, such as *Me96* or *Mo99*, never held it and participated intermittently or only briefly. The absence of rules to regulate the participation or close of play made the boundary of SOP membership unclear, in contrast to play-tag of human children in which the boundary is normally clear and regulated by such rules.

The difference in the ways to participate in SOP among each juvenile is considered to reflect the variations of their interests in a particular object they targeted. When an object attracted many juveniles at the same time, the SOP would be observed to be "excited or fevered." On the other hand, the object in which they lost their interest might be abandoned, and SOP would cease naturally.

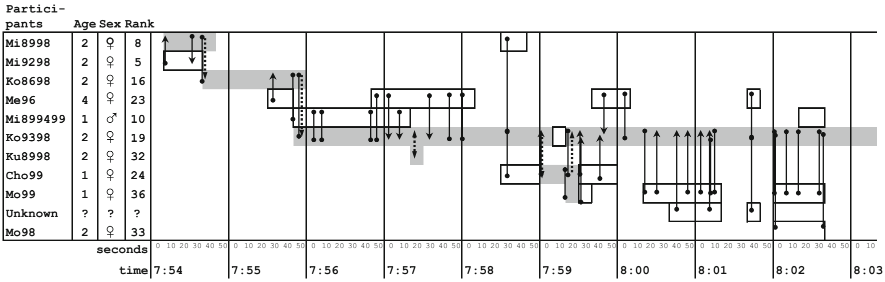

**Fig. 18.3** The *left side* of the figure displays each participant, and the time axis for each individual extends from left to right. For convenience, bouts are displayed in 10-s units. *Hatched bars*, individuals holding the object (a broken, transparent plastic cup); *white bars*, individuals confirmed or estimated to be within a 3-m radius of the holder during that time unit; *vertical solid arrows*, play-chasing between a holder and nonholder(s) and the direction of chasing (the individual from which the *arrow* originates indicates a chaser, and the individual toward which the *arrow points* is the chasee); *vertical solid lines*, interactions other than play-chasing; *vertical dotted arrows*, transference of the cup among individuals (the *arrow* indicates the previous cup holder; the *arrowhead* points toward the succeeding cup holder). [From Fig. 2 in Shimada (2006), with kind permission of Springer Science+Business Media]

Although the regularity of the interaction represented by PCT is one of the most prominent features of SOP in Arashiyama, juveniles would never be forced to join in, leave, or obey any rules, that is, SOP were substantially "free" activity. They, however, generated regulative interaction once they joined in.

### *18.5.5 Future Perspective to the Study of Play*

Any ethologist trying to study animal play behavior needs to find questions in the phenomena of play that are worthy of research and logical ways to solve the questions they identify. However, there are two inevitable and substantial difficulties in the study of animal play behavior to which no one has succeeded in giving clear solutions thus far: the definition and the function of play.

In this paper, I have used my study of SOP among juveniles in Arashiyama as an example of a logical "detour," not addressing these problems directly, and to clarify the proximate mechanism that make the interactive features of SOP possible. In this process, I discussed some interesting innovative views of SOP, although some of these are based on suppositions and need to be verified by future research.

As far as the study of animal play behavior is concerned, watching the phenomena well and finding a "detour" may sometimes be more fruitful than trying to stick to the ground theory or methodology of behavioral ecology and abandoning research.

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# Topic 7: Japanese Macaque Society as a Complex Adaptive System

**Nobuyuki Kutsukake**

## 19.1 Introduction

The formation and maintenance of valuable (i.e., fitness-generating) relationships (Silk et al. 2003) are critical factors influencing individual strategy and decision making in primates (Cords 1997). Here I briefly explain the strategic use of social behavior to cultivate and maintain valuable relationships in Japanese macaques (*Macaca fuscata*) and suggest the possibility of applying "complex adaptive systems" theory to aid our understanding of complex social dynamics in this species. Valuable relationships, which are characterized at the level of social interaction by frequent association, proximity, co-feeding, and grooming, are not distributed randomly within a group, but are clearly dependent on the sex combination of dyads. Valuable relationships are relatively rare between males but common between females, reflecting a social system with male dispersal and female philopatry. Valuable relationships usually occur among related females, leading to the assumption that the ultimate background of such relationships is nepotism (Kurland 1977). However, careful consideration of the payoffs involved in social behavior suggests that relatedness is not the sole and consistent factor shaping valuable relationships, and that the mutualism has been underestimated in valuable relationships (Chapais 2006).

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## 19.2 Heterosexual Friendships

An interesting social dynamic is seen in the persistent affiliative relationship between an unrelated male and female, the so-called peculiar proximate relations (Takahata 1982; Hill 1999; see also Chap. 11) or heterosexual friendship (Kutsukake and Hasegawa 2005). The ultimate function of these relationships has not been conclusively revealed in Japanese macaques. The relatively rare occurrence of infanticide in Japanese macaques (Soltis et al. 2000; Yamada and Nakamichi 2006) suggests that, as has been proposed in baboons, protection from infanticidal males is not the primary function of this relationship. No studies have used paternity tests to determine whether males sire offspring with friendly females; therefore, it is still unknown whether reproductive purposes explain the friendly relationship. In wild groups, males are responsible for maintaining friendly relationships (Hill, unpublished; in Hill 1999). In contrast, in a provisioned group in which interindividual competition and power asymmetry are exaggerated relative to wild groups, the maintenance of friendly relationships is the responsibility of females. This intraspecific variation suggests that a plausible explanation for the formation of friendly relationships by females is the protection provided by a friendly male from aggression by other group members and other relevant benefits such as priority access to resources (Hill 1999). Supporting this idea, the maintenance of friendly relationships is dynamic and changes according to the costs and benefits that a given social relationship provides. In one extreme case, friendly females ended their friendly relationships with the defeated alpha male when the alpha male was overthrown by a beta male (Kutsukake and Hasegawa 2005; see also Nakamichi et al. 1995a for a case in which an old alpha male maintained his position by support of a friendly alpha female when he was attacked by a beta male). Still, it remains unknown why males, but not females, maintain friendly relationships in wild groups.

## 19.3 Grooming, Coalition, and Alliance

Valuable relationships are cultivated and maintained by grooming. Grooming is commonly seen among related females (Furuya 1957; Yamada 1963; Koyama 1991; Takahashi and Furuichi 1998; Schino 2001; Nakamichi and Shizawa 2003). Grooming is reciprocated (Muroyama 1991; Schino et al. 2003) or used to gain other social benefits (i.e., support: Schino 2007; Schino et al. 2003, 2007a; Ventura et al. 2006). One of the most important social benefits is agonistic support, or coalition and alliance formation during within-group conflicts. Coalition and alliance formation play critical roles in the determination of dominance rank among females (matrilineal rank inheritance: Kawai 1958; Kawamura 1958; Koyama 1967, 1970; Takahata 1991; Nakamichi et al. 1995b). Chapais and colleagues conducted a series of experiments showing that mutual selfishness dominates other mechanisms such as reciprocal altruism or even nepotism in decision making during coalition formation (Chapais et al. 1995; reviewed in Chapais 1992). That is, a coalition is most likely

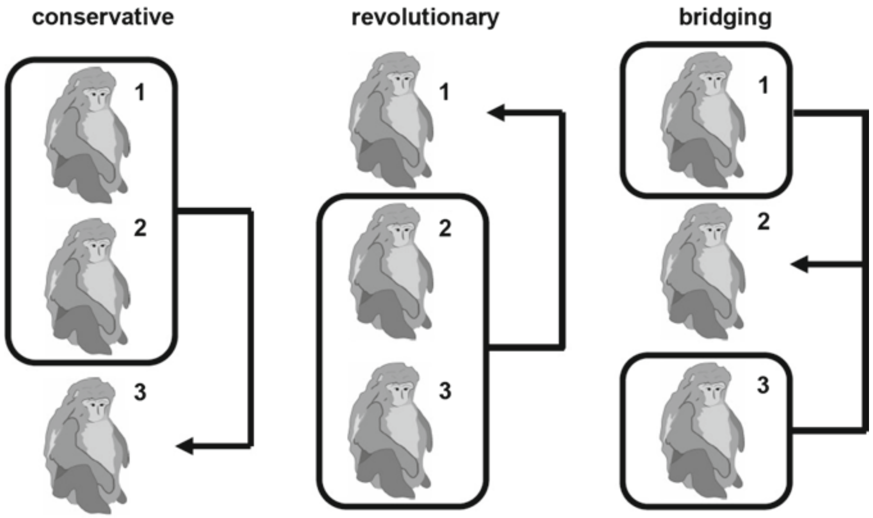

**Fig. 19.1** Three types of within-group coalition formation: conservative, revolutionary, and bridging (Chapais 1995). The *number* of each individual indicates its dominance rank. The *arrows* indicate coalitionary aggression

to be formed among higher ranking individuals against a low-ranking individual (Fig. 19.1, conservative coalition; Chapais 1995). However, an alpha male and mothers frequently support the weaker individual in a conflict (Watanabe 1979). Also, males commonly support the females with whom they have friendly relationships when the females attack or are attacked by other group members, which occasionally results in stable dominance rank reversal among females (Chapais and Lecomte 1995; Kutsukake 2000). Individuals often recruit agonistic support from other group members, and this choice of target is determined by relative dominance rank (individuals ranking higher than the opponent are preferentially solicited) and relatedness between a recruit and the opponents (individuals unrelated to the opponents are preferentially solicited) (Schino et al. 2006). Revolutionary coalitions (Fig. 19.1, a coalition between subordinates against a dominant) are rarely formed, but are not completely absent in this species; Kutsukake and Hasegawa (2005) reported a rare event in which related males competed for dominance using conservative and revolutionary coalition formation after an alpha male was overthrown.

## 19.4 Reconciliation and Aggression

Even if disturbed, valuable relationships can be regulated by reconciliation following aggression (Arnold and Aureli 2007). Reconciliation repairs the damaged relationship and reduces the stress caused by aggression (Kutsukake and Castles 2001). In Japanese macaques, related individuals reconcile more frequently than do unrelated individuals (Schino et al. 1998; Kutsukake and Castles 2001; Majolo et al. 2009), suggesting that reconciliation plays a particularly important role in preserving the social benefits of valuable social relationships (Aureli 1997). Postaggression stress reflects the value of social relationships; the damage to social relationships between related group members increases social stress (as measured by the rate of self-directed behaviour) for victims (Kutsukake and Castles 2001). Furthermore, the stresses exhibited by aggressors and victims are positively correlated (Schino et al. 2007b). This variation in postaggression stress explains the proximate aspects of the higher conciliatory tendency among related dyads as compared to unrelated dyads (Aureli 1997). It should be noted that relatedness and the value of social relationships are not the only factors that are predicted to be associated with the occurrence of reconciliation; therefore, quantified characterization of social relationships is necessary to understand the multidimensional aspects of social relationships (Majolo et al. 2009).

In addition to these affiliative, altruistic, and cooperative interactions, aggression is used strategically to derive benefits from social interactions. Generally, aggression in primates is caused by competition for limited resources. However, in Japanese macaques, most cases of aggression occur suddenly and seem to be unrelated to the immediate social context. Thus, it is often difficult for researchers to determine the immediate reason for the aggression. Although aggression has received much attention in classic studies of Japanese macaques, our understanding of aggression is still incomplete because these studies considered all types of aggression together, ignoring the heterogeneous nature of aggression. Functional and contextual analyses such as those of social behavior before and after aggression must be both informative and useful if we are to understand the social functions of aggression and to formally test the strategic aspects of aggression. One of the best examples of such an analysis is that of postaggression behavior. Aggression destabilizes not only the relationships between the opponents but also those among other group members. Once aggression occurs, group members, regardless of whether they were involved in the aggressive interaction, engage in various types of social interaction. Redirection of aggression by a victim of aggression may function as revenge toward relatives of the aggressor or reinforce the dominance hierarchy (Aureli et al. 1992). Victims of aggression are likely to be attacked again by both the initial aggressor and other group members (Kutsukake and Castles 2001). Following the original aggression, an aggressor may also use aggression as a social tool with which to suppress a possible future opponent (Rizaldi and Watanabe 2008). These strategic uses of aggression suggest that aggression is not the result of direct competition for limited resources, but has sophisticated social purposes, enhancing dominance and regulating social relationships.

## 19.5 Modeling Social Dynamics in Japanese Macaques

The Japanese macaque society is a system in which each individual employs adaptive decision making to maximize inclusive fitness under the given social constraints, and as a result, social relationships with different characteristics are shaped and regulated through the interactions among group members. This description means that the formation and regulation of social relationships are not determined by the interplay of decision making between two individuals but should be considered from a more global perspective (Kutsukake 2009). To model such complex systems, it might be necessary to introduce a nonreductive framework in addition to the traditional reductive approaches. One of these frameworks is the "complex adaptive system" (Miller and Page 2007). This computational agent-based model sets multiple agents, each of whom has an adaptive decision-making algorithm and who interact with one other. Using this framework, the outputs of the model are not always a deterministic summation of the model subcomponents; stochastic and nonlinear outcomes can emerge. Therefore, it is possible to investigate how the local interactions among agents result in nonlinear outcomes. Agent-based models have been applied to primate behavior and are applicable to the analyses of social dynamics discussed here (Kohler and Gummerman 2000; Hemelrijk 2005). In the case of social partner choice in the formation of a valuable relationship, for example, Seyfarth (1977) formulated social competition between grooming partners among females and suggested that stable grooming relationships emerge between females occupying adjacent dominance ranks. Despite the great success of the Seyfarth model for explaining social dynamics (Schino 2001), this model does not explain the emergence of a few subordinate individuals who form stable relationships or heterosexual friendships with higher-ranking individuals (Fig. 19.1; a bridging coalition) and rise in the dominance hierarchy (Kutsukake 2000). In other words, dominant individuals who should be attractive social partners are occasionally available for strong social relationship formation with subordinates. These observations are consistent with the low cohesiveness of dominance positions and social relationships in low-ranking kin-groups in Japanese macaques (Koyama 2003; see also Kutsukake 2000 for emigration of subordinate females from a natal group). These exceptions do not mean that the Seyfarth model is inappropriate in this species. Rather, it is interesting to ask under what social situations some subordinate individuals succeed at forming a bridging coalition and outrank individuals that are expected to be dominant. Multiagent models such as the complex adaptive system might help answer this question by simulating the distribution of valuable relationships under different social parameters, such as rank-related benefits, number of group members, and asymmetry of resource holding power. This is only one example of how a nonreductive framework can be applied and can promote our understanding of primate social behavior. An important point is that modeling necessitates realistic social parameters and information on decision-making patterns, ideally obtained from empirical studies under various different ecological, social, and demographic contexts. Furthermore, experimental data are the most reliable and powerful for establishing biologically valid models. Given that Japanese macaques have been studied at many field sites and in captive settings, and that experimental studies have examined their social dynamics (Chapais 1992), an abundance of empirical data on intraspecific variation has accumulated. Although a complex adaptive system and agent-based model have not been applied to Japanese macaques (and are not common in primatological studies), Japanese macaques have great potential to be the first primate species in which complicated social dynamics are modeled based on empirically validated assumptions and parameters.

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