Chapter 5
Japanese Macaques: Habitat-Driven Divergence in Social Dynamics

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Abstract Japanese macaques (*Macaca fuscata*), among the most intensively studied nonhuman primates in the world, live in a wide range of habitats in the Japanese archipelago. They offer us interesting examples on how habitat affects the social and population dynamics of long-lived animals. Studies of provisioned groups up to the 1970s revealed the basic social structure of Japanese macaques, characterized by a female-philopatric matrilineal society. Subsequently, two long-term study sites were established to study the nonprovisioned wild population in warm-temperate evergreen and cool-temperate deciduous forests in lowland Yakushima and Kinkazan, respectively. In both sites, a population increase was observed during the first decade of the long-term study, which was accompanied by group fission. An abrupt population decline resulting from external and environmental changes was then observed in both sites. The biggest difference between lowland Yakushima and Kinkazan is the inequality among groups and the stability of groups, which results from differences in the intensity of intergroup competition. In lowland Yakushima, macaques are under intense intergroup competition, and small groups suffer from low birthrate; finally, they may become extinct. In Kinkazan, intergroup competition is not intense, and there are no group size-dependent population fluctuations. This difference is believed to be a result of the more clumped distribution of high-quality foods in Yakushima compared to Kinkazan. In Yakushima, another long-term study site has been established recently in the high-altitude coniferous forest. In the future, Yakushima may offer us a rare opportunity to study the long-term social and population dynamics and within-population interchange of groups in a heterogeneous habitat.

Keywords Birthrate • Fruit production • Group extinction • Habitat • Japanese macaques • Mass mortality • Population dynamics • Socioecology

5.1 Introduction

Japanese macaques (*Macaca fuscata*) live over a wide range of habitats in Honshu, Shikoku, and Kyushu Islands and some small islands in the Japanese archipelago habitats (Fig. 5.1). In the lowland forest of Yakushima, which is the southern limit of the distribution of the species, macaques live in an evergreen forest mixed with subtropical species. The temperature rarely drops below 10 °C, even in winter. In contrast, in the snowy Shiga Heights in Nagano Prefecture, which is probably the coldest habitat for wild primates, the temperature often drops below –20 °C and the snowfall reaches several meters in depth. Shimokita Peninsula is the northern limit of distribution of not only Japanese macaques but also all the nonhuman primates. Japanese macaques also live in high mountains: they use alpine grasslands around the summit of Mt. Yarigatake (3,050 m) (Izumiyama et al. 2003). Some of the populations are highly dependent on crops (Izumiyama et al. 2003). Considering that primates are originally tropical animals, the extensiveness of the habitat occupied by Japanese macaques is surprising.

Fig. 5.1 Study sites of Japanese macaques

Japanese macaques are undoubtedly the species that has been studied for the longest period among primates. The study of wild Japanese macaques started on 3 December 1948. On that day, Kinji Imanishi and his two undergraduate students at Kyoto University, Shunzo Kawamura and Jun'ichiro Itani, conducted an expeditionary survey in Koshima, a small islet in Miyazaki Prefecture, Kyushu. Since then, field studies of Japanese macaques have been conducted in various sites in Japan. Japanese primatologists were particularly interested in the evolution of social structure, and they have accumulated data based on individual identification and long-term observations. The long-term data set of various study sites, combined with the extensive habitat diversity of this species, offers us a rare opportunity to examine the effect of habitat on long-term social dynamics. Studies on intraspecies variation are important to assess how flexibly animals can match their social behavior to the current environment (Nakagawa et al. 2010). Socioecological models mainly focus on interspecies variations (Sterck et al. 1997), but it remains unclear how much those models are applicable to explain intraspecies variations.

Here, I compare the social dynamics of Japanese macaques in various sites in Japan, including both provisioned and nonprovisioned populations. In particular, I examine the two long-term study sites in detail: Yakushima and Kinkazan. These two sites are among the habitats for Japanese macaques where any form of artificial habitat disturbance is minimal, such as provisioning, deforestation/aforestation, hunting, and crop raiding. In both sites, multiple groups of Japanese macaques have been individually identified and observed for more than 30 years. The two habitats are contrasting: warm-temperate evergreen forest in Yakushima and cool-temperate deciduous forest in Kinkazan, which are the two main types of Japanese macaque habitat. First, I summarize the social organizations and social dynamics of provisioned Japanese macaques. Second, I describe the social dynamics observed in nonprovisioned Yakushima and Kinkazan in detail and examine the similarities and differences. Third, I explore the habitat characteristics that may affect the differences in the social dynamics between the two sites. Finally, I introduce an ongoing project to compare the spatial variations in the social and population dynamics of Japanese macaques in Yakushima that are living at different altitudinal zones.

5.2 Social Dynamics of Provisioned Japanese Macaques

Most Japanese macaque studies during the early period of their research were conducted among provisioned groups. Japanese macaques were hunted as game until 1947, so they were afraid of humans when researchers began observations in late 1940s. Provisioning was the only way to habituate the macaques to human observers. By the 1970s, Japanese macaques were provisioned in more than 30 sites, including the long-term study sites in Koshima, Takasakiyama, Arashiyama, and Katsuyama. Most of the provisioning was performed by cities, prefectures, or travel companies to attract tourists.

The researchers found a similar social organization in the various study sites of provisioned Japanese macaques. After the 1980s, these similarities were found to be largely applicable to nonprovisioned groups. Japanese macaques form matrilineal social groups (Kawamura 1958; Furuichi 1985). Females stay in their natal group for all their life (Yamagiwa and Hill 1998). There are linear and stable dominance hierarchies within both sexes, and females inherit their social rank from their mothers (Koyama 1967; Hill and Okayasu 1995). Females usually confine their daily social interactions, such as grooming, to their maternal kin (Yamada 1963; Takahashi and Furuichi 1998). When the group fissions, females persistently associate with their kin (Furuya 1969; Koyama 1970; Oi 1988). In contrast, males disperse their natal groups during puberty, and adult males tend to stay in a group for only a few years (Fukuda 1982; Sprague et al. 1998). Males can avoid inbreeding by repeated emigration and immigration.

As a consequence of their enhanced food availability, provisioned Japanese macaques increased in population size. The population size in Takasakiyama was around 160 before provisioning began in 1953 and increased 1.093 times every year during the period from 1953 to 1975 (Sugiyama et al. 1995). The population reached more than 2,000 individuals, forming three groups, in 1979; the largest group included more than 1,200 animals. In many other provisioned populations, such as Arashiyama and Shiga Heights, group size increased to more than 200, which was larger than the maximum size reported for nonprovisioned groups (160 in Takasakiyama before provisioning started) (Takasaki and Masui 1984). Some of the sons of high-ranking females did not emigrate from their natal groups after they reached maturity (Kutsukake and Hasegawa 2005). The extreme concentration of high-quality foods enabled the macaques to maintain extraordinarily large group sizes and allowed some males to remain with their natal groups.

Because of the difficulty in managing extraordinarily large groups, the amount of provisioned foods was decreased by the managers around 1970. Abrupt changes in food availability significantly affected the group dynamics of the provisioned groups. In Mt. Ryozen, central Japan, one group of Japanese macaques was provisioned from 1966 to 1973. After provisioning ended, the birthrate decreased, infant mortality increased (Sugiyama and Ohsawa 1982b), and group desertion of females was frequently observed (Sugiyama and Ohsawa 1982a). If female desertion is defined as leaving the original group for more than 1 month without either serious illness or injury, there were 14 cases and all the 22 female deserters were 5 or more years old. The proportion of female deserters was 9.48 %/year. Several females left their group for 1 year and were sporadically observed to range alone. Some of them returned to their group, but some of them did not. In May 1978, 11 orphan subadult and juvenile females, who were deprived of their mothers by large-scale capture in November 1977, deserted the group and formed a new home range 4 km away from their original home range. The new group was composed of both high- and low-ranking individuals, and some of them left their maternal siblings in the original group. Thus, it was different from the usual group fission, in which monkeys separate with their kin. Sugiyama and Ohsawa discuss that female desertion of the group occurs when food supply becomes insufficient compared to group size.

Studies of provisioned groups revealed the basic social structure of Japanese macaques, characterized by a female-philopatric matrilineal society. The studies also clarified that macaques respond to abrupt external changes, such as large-scale capture and sudden decrease of food availability, in a different way from their ordinary pattern, such as philopatry and strong bonds with maternal kin. However, all these changes were artificial, so it remained unknown whether these changes occur in natural conditions.

5.3 Social Dynamics in the Lowland Forest of Yakushima

Yakushima is an island in southwestern Japan (30°N, 131°E) that occupies an area of 503 km^2 (Fig. 5.2). The highest peak is Mt. Miyanouradake (1,936 m a.s.l.), which is the second highest mountain in western Japan. The mean annual temperatures are 20 °C and 12 °C, and the mean temperatures of the coldest month (February) are 11 °C and 3.4 °C in the forests at altitudes of 100 m and 1,050 m, respectively (Tagawa 1980; Hanya 2004a). Kimura and Yoda (1984) classified the vegetation of Yakushima into five zones. (1) In the subtropical warm-temperate transitional zone (0–100 m a.s.l.), subtropical plants such as strangler figs (*Ficus superba* and *Ficus microcarpa*) are mixed with warm-temperate evergreen broad-leaved trees. (2) In the warm-temperate evergreen broad-leaved forest zone (100–800 m a.s.l.), warm-temperate evergreen broad-leaved trees (e.g., *Castanopsis cuspidata*, *Quercus salicina*, *Distylium racemosum*) are dominant. (3) In the warm-temperate/cool-temperate transitional forest zone (800–1,200 m a.s.l.), warm-temperate evergreen broad-leaved trees such as *Quercus acuta*, *Q. salicina*, and *D. racemosum* are mixed with

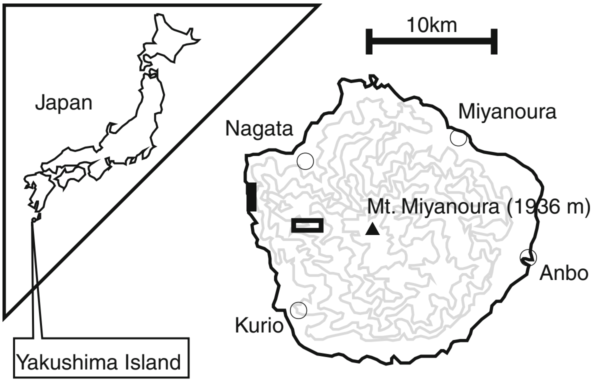

Fig. 5.2 Yakushima Island. *Closed square* indicates the long-term study site in the western lowland forest. *Open square* indicates the newly established study site in the coniferous forest. *Open circles* are major villages. Contours were drawn every 300 m in elevation

conifers such as *Cryptomeria japonica*, *Abies firma*, and *Tsuga sieboldii*. (4) In the cool-temperate zone (1,200–1,700 m a.s.l.), conifers such as *C. japonica*, *A. firma*, and *T. sieboldii* are dominant. (5) In the summit dwarf scrub (1,700 m), tall trees cannot grow, and a bamboo, *Pseudosasa owatarii*, covers the summit area. Japanese macaques inhabit all these zones, but their population density is highest in the lowland forest (<400 m a.s.l.), and did not differ among other zones. Difference in annual fruit production is the main factor affecting the altitudinal variations in macaque density (Hanya et al. 2004b).

After the pioneering survey by Kawamura and Itani in 1952, long-term study of Japanese macaques in Yakushima started in 1974, in the western lowland forest of Yakushima. Although large-scale forest development was ongoing all over Japan at that time, wide areas of natural vegetation still remained in Yakushima. At the same time, thanks to the hunting tradition using of traps, not guns, to capture macaques, Yakushima macaques were not afraid of humans even before intensive observation began. In 1974–1976, young Japanese primatologists studying at various field sites gathered in Yakushima and conducted a census of Japanese macaques three times. They found that the population density in this area was highest for this species (33/km^2) (Maruhashi 1982), and macaques were relatively habituated to humans. Among them, Tamaki Maruhashi, a graduate student at Kyoto University, and his colleagues habituated and identified all members of the Ko group in 1974, which was the first successful case for nonprovisioned Japanese macaques. Since then, intensive observation of multiple groups of Japanese macaques has continued.

Japanese macaque groups in the western lowland forest of Yakushima changed in a very dynamic way (Fig. 5.3). The Ko group, which was first habituated by Maruhashi, contained 47 animals in 1976. The Ko group fissioned twice within 3 years of the beginning of the research period. One of the daughter groups fissioned again in 1987, forming four groups. Six group fissions were observed among the Ko lineage and their neighboring groups during the period 1974–1987 (Sugiura et al. 2002). Increase

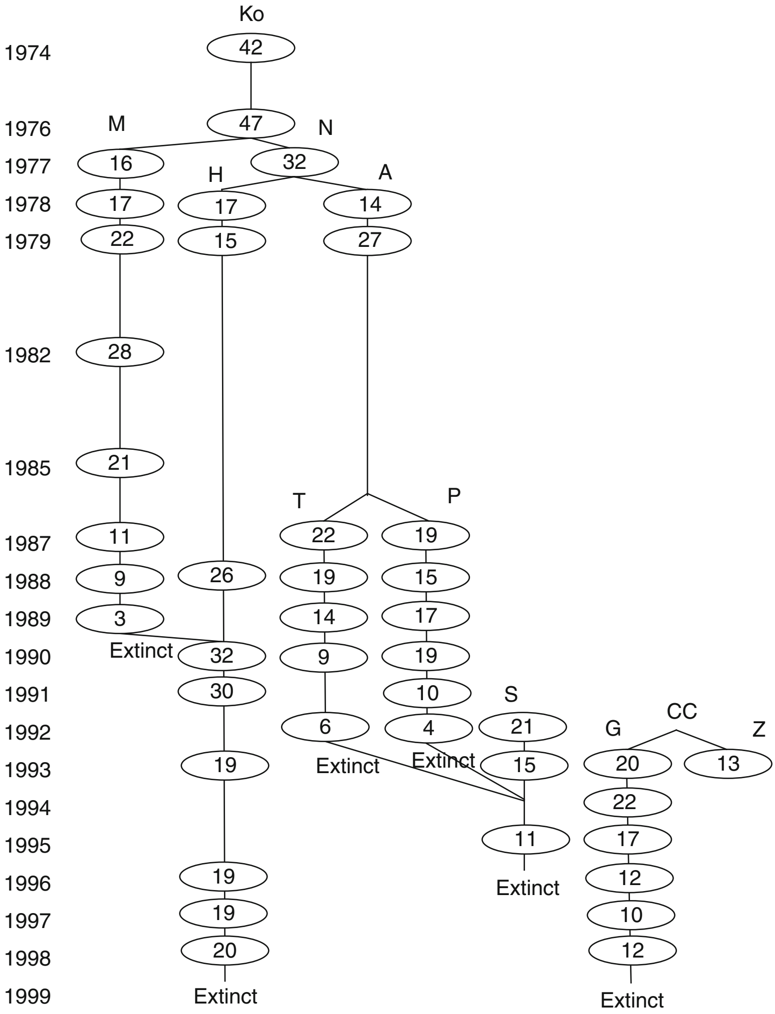

Fig. 5.3 Dynamics of Ko lineage and its neighboring groups of Japanese macaques in the western lowland forest of Yakushima. *Encircled numbers* are numbers of individuals. (Modified from Hanya 2002)

of group numbers probably resulted from the increase in population density. The population density at the onset of the study was 33 macaques/km^2 (Maruhashi 1982); however, it increased to 62–100/km^2 in 1993 (Yoshihiro et al. 1999). Yakushima macaques were hunted until the end of the 1960s for biomedical experiments, maintaining the population below the carrying capacity of their habitat. The population was probably recovering during the early period of the long-term research.

In contrast, after 1988, group fission rarely occurred, and some groups became smaller and finally became extinct. The first group extinction occurred in the M group,

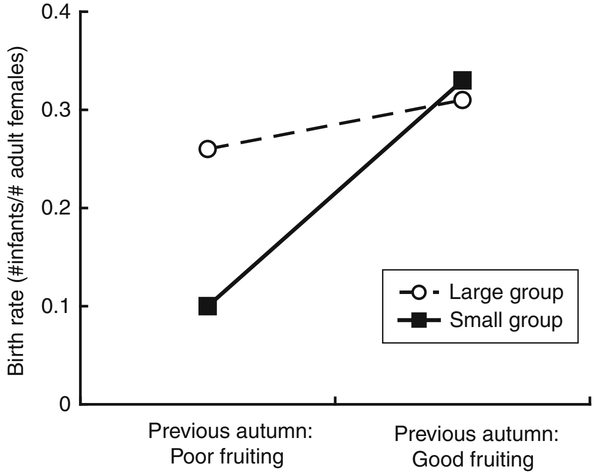

Fig. 5.4 Effect of group size and fruit production on birthrate of Japanese macaques in the western lowland forest of Yakushima. (Modified from Suzuki et al. 1998)

one of the daughter groups of the Ko group. Since the fission from the Ko group in 1977, the M group increased to 28 individuals in 1982. Then, the group size decreased gradually, and its home range also became smaller. In 1989, one adult male, one adult female, and her adolescent daughter were the only members of the M group. During the mating season of this year, the male emigrated, and the two remaining females joined the neighboring H group as the lowest-ranking animals (Takahata et al. 1994). Japanese macaque females were believed to stay in the natal group for all their life except when the group fissions; this was the first case of group fusion observed in Japanese macaques. In the early 1990s, other daughter groups of the Ko lineage, T and P, also decreased in number, and the few remaining females fused with the neighboring S group. In 1995, the S group also decreased in size and then disappeared (Sugiura et al. 2002).

Group extinction was influenced by intergroup competition. In Yakushima, intergroup relationships were antagonistic (Saito et al. 1998), and a dominant–subordinate relationship was apparent when the group size differed considerably (Sugiura et al. 2000). When the two different-sized groups encounter each other, the smaller group usually flees only when they notice the larger group by vocalization. Before their extinction, the home range of the M group was so small that there was no home range that they could use exclusively. They wandered as if they were escaping from the larger neighboring H group (Takahata et al. 1994). The T and P groups were also driven away by the neighboring CC group, which included more than 30 individuals and had migrated from an east mountainous area (Sugiura et al. 2002). As a result of intergroup competition, the birthrate of small-sized groups was smaller than in large-sized groups (Takahata et al. 1998). This difference was intensified when fruit production was poor (Fig. 5.4) (Suzuki et al. 1998). When the group becomes small, few infants are born, and the group becomes even smaller, and finally it vanishes.

In early 1999, a mass mortality of Japanese macaques occurred in the long-term study site in Yakushima. At that time, all individuals in five groups were identified. During the absence of observers from January to April of that year, 56 % of the animals disappeared, including all the members of the H (the last remaining Ko lineage) and G groups (Hanya et al. 2004a). Mass mortality among Japanese macaques had been reported in northern Japan as a result of heavy snow and an extremely cold winter (Izawa 1988). However, the lowland forest of Yakushima is the warmest habitat, harboring rich food resources and the highest population density for this species (Hanya et al. 2004b).

Although the direct cause of this mass mortality is not known, exceptionally poor fruit production in the preceding autumn certainly had an effect. During the 14 years from 1988 to 2001, fruit production in the autumn of 1998 was the poorest, only one-tenth of that in 1993, when the fruit production was the greatest. In fact, fruits produced in autumn usually remain until January and February. However, in this year, all fruits were consumed in December, and the macaques then ate mature leaves (Hanya et al. 2004a). Mature leaves are nutritionally lower in quality than fruits, and it is difficult for the macaques to satisfy their energy requirements even if they eat up to their gut capacity (Mori 1979). The fresh carcasses collected at the early stage of mass mortality contained little deposited fat (Hanya et al. 2004a), suggesting that the nutritional condition was bad in this year. Although it is very likely that there were other direct causes, such as disease, the poor fruit crop and the resulting poor nutritional conditions were the important background of this mass mortality.

Another important aspect of this mass mortality was local concentration (Fig. 5.5). The two extinct groups were neighbors to each other, and there was a pattern that mortality decreased with increasing distance from the two extinct groups (Hanya et al. 2004a). Although the cause of this pattern remains unknown, prevalence of epidemic disease may explain this. Whatever the cause, the imbalance of mortality among groups has changed intergroup relationships. For example, the K group, which was not affected by the mass mortality, expanded their home range northward, into the center of the mass mortality area, and fissioned a few years later. The home ranges of the extinct groups were occupied by other groups within only 2 years.

As a result of these social and population changes, all the Ko lineage groups have disappeared. Now the home range is occupied by other groups, which migrated from the east (vertical migration from higher altitude) or south (horizontal migration from the lowland). The long-term study of Yakushima revealed that the Japanese macaque groups are under intense competitive relationships. Japanese macaque groups fluctuate from both external (e.g., mass mortality) and internal (e.g., intergroup competition) causes and are not stable over the long term.

5.4 Social Dynamics in Kinkazan

Kinkazan is an island that lies 700 m offshore Oshika Peninsula, Miyagi Prefecture, northern Honshu. Its area is 10 km^2 with the highest peak of 445 m a.s.l. The mean annual temperature is 11 °C. The island is rarely covered with snow, although it

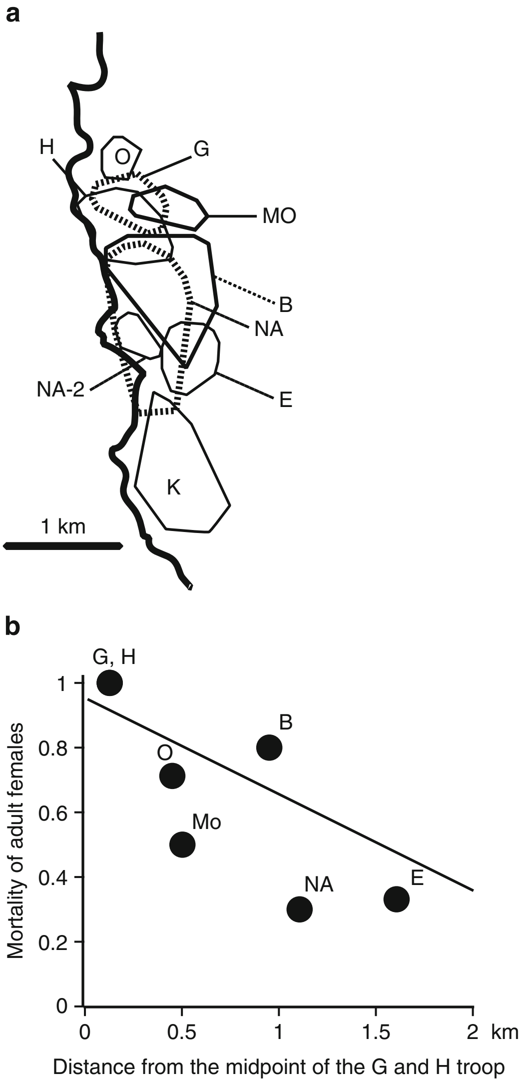

Fig. 5.5 (**a**) Distribution of Japanese macaque groups in the western lowland forest of Yakushima in 1998, before mass mortality occurred. (**b**) Relationships between the adult female mortality of each group during the mass mortality in 1999 and its distance from the two extinct groups (G and H). (Modified from Hanya et al. 2004a)

occasionally snows on cold winter days. The island is covered with a mixed forest of deciduous and coniferous trees, such as *Fagus crenata*, *Abies firma*, and *Pinus thunbergii*. However, saplings of woody plants have rarely developed into mature trees recently because of high feeding pressure by sika deer. Grasslands of *Zoysia japonica*, *Miscanthus sinensis*, and other grasses widely cover some parts of the island (Agetsuma and Nakagawa 1998).

In Kinkazan, some short-term surveys of Japanese macaques were conducted in the 1960s and 1970s. In 1982, Kosei Izawa started a long-term study of Japanese macaques on this island when he was assigned to a professor at Miyagi University of Education, a nearby university from Kinkazan. With the aid of his colleagues and his undergraduate students, he has conducted a census of Japanese macaques three times a year. Because of the small area and clear visibility, it was possible to count all the population in this island. Detailed behavioral observations based on individual identification were also conducted by various researchers.

Population changes in Kinkazan have been summarized by Izawa (2005). In Kinkazan, there was only one group in the 1960s. If the 1960s and 1970s are included, when only intermittent data are available, five fissions occurred in 42 years. Among them, two group fissions occurred after the long-term study started in 1982. No group extinction was observed. Mass mortality occurred in the winter of 1984 winter as a result of heavy snow and exceptional cold. During this year, the population decreased from 270 to 180. The population gradually recovered after that, reaching 294 in 1994. Subsequently, the population began decreasing gradually, to 217 individuals in 2003. Even when the population size decreased, there was no tendency for only a particular group to decrease in size. Intergroup relationships are not antagonistic. The frequency of intergroup encounters was one third of that in Yakushima, in accord with the differences in group density (Sugiura et al. 2000). When two groups encountered, no apparent social interactions were observed (Saito et al. 1998). There was no tendency for the birthrate to be smaller for small groups than large groups (Takahata et al. 1998).

5.5 Similarities and Differences in the Social Dynamics in Yakushima and Kinkazan

There are both similarities and contrasts in the social and population dynamics of Japanese macaques between the two study sites. In both sites, population increase was accompanied by group fissions. In Yakushima, group fission occurred frequently during the period when population density doubled (1970s–1980s). In Kinkazan, population size was less than 70 in 1962 and increased to almost 300 in 1994. The number of groups also increased, from one to six, during that period. It is suggested that there is a limit to the maximum group size, which is probably around 50 in Yakushima and 80 in Kinkazan. These numbers are much smaller than the group size of most of the provisioned groups. Increased within-group competition and the difficulty in maintaining group spread are likely to be key factors limiting maximum group size; however, there are no quantitative data to suggest why the maximum group size differs among habitats. Another similarity is that a sudden population decrease from external and environmental changes can occur over a long time. The effect can be as great as killing one third of the entire population, as in Kinkazan, or local but so large as to make multiple groups extinct within a few months, as in Yakushima. Both the long-term studies tell us that the effects of these rarely occurring events are not negligible over the long term.

The biggest difference between Yakushima and Kinkazan is the inequality among groups and the stability of the groups, which result from the difference in the intensity of intergroup competition. In Yakushima, macaques are under intense intergroup competition, and small groups suffer from low birthrate and finally may disappear. In Kinkazan, intergroup competition is not intense, and there are no group size-dependent population fluctuations. Maruhashi et al. (1998) compared the home range structure between the two habitats. In Yakushima, (1) food tree density was higher, (2) interfeeding bout site distance was shorter, (3) daily travel distance was shorter, (4) home range size was smaller, and (5) the macaque groups shared a greater proportion of their home range with neighboring groups compared to Kinkazan. Consequently, food distribution is more clumped, and thus the quality of the home range is more worth defending in Yakushima than in Kinkazan. Intergroup competition is enhanced in Yakushima compared to Kinkazan by the high frequency of intergroup encounters that result from higher group density and greater overlap in home range between neighboring groups.

5.6 Linking Environmental, Population, and Social Changes: Commencement of Another Long-Term Research Project

The two long-term study sites successfully revealed the variability of social dynamics of Japanese macaques under natural conditions. However, we still cannot understand the social dynamics as an ecological process of population dynamics because quantitative data on habitat changes are lacking. In addition, continuous data on population density are not available in Yakushima.

In both Yakushima and Kinkazan, the increase of population size up to the early 1980s was probably related to past hunting pressure. In Yakushima, for example, it is said that 950 macaques were exported from Yakushima during the period of 1950–1969 (Azuma 1984). However, no record remains where in Yakushima and how many were captured each year, so it is difficult to estimate how much impact the hunting had on macaque populations. In Yakushima, it is also said that secondary vegetation along a road that was opened in 1967, a few years before the start of the long-term research, changed in succession (Maruhashi 1984). It is possible that food availability, and thus carrying capacity, changed with vegetational succession, but there are no quantitative data to examine. In Kinkazan, the population has been gradually decreasing since the late 1990s (Izawa 2005). It is believed that high grazing pressure by sika deer is degrading the island vegetation, and recent strong typhoons, which damaged many old large trees, have accelerated the deterioration (Izawa 2005). However, there are no quantitative data on the vegetation changes for the past few decades.

In Yakushima, in spite of the diversity of habitat along the elevational gradient, studies of Japanese macaques were largely conducted only in the western lowland forest until the 1980s. In 1989, Shinichi Yoshihiro organized a census team (Yakushima Macaque Research Group; Yakuzaru-Chosa-Tai) to study distribution of macaque groups in various areas in Yakushima, including higher mountainous zones and around the coastal villages, where macaques raid crops. Every summer, more than 40 volunteers, who are mostly inexperienced undergraduate students, joined the census. From 1990 to 1993, they studied the lowland and clarified that population size in that area (127 km^2, 1–2 km from the coast) was 2,000–3,850 macaques (Yoshihiro et al. 1998). From 1994 to 1997, they studied the vertical distribution of Japanese macaques in the western area, which is the only area where natural vegetation is preserved from the coast to the summit (Yoshihiro et al. 1999; Hanya et al. 2004b).

After the completion of the island-wide distribution survey, the census team set up a new long-term study site in the coniferous forest in the western area. They established a census area of 7.5 km^2 and have studied group density by a modified point census, a method that they devised (Hanya et al. 2003b). They also studied the composition of several identified groups in their study site. In 2000, four groups were identified, and one of them fissioned in 2005. Based on the results of the census team, I identified all the individuals in one group among them (HR group) and conducted detailed behavioral observation for 1 year from April 2000. I also set a permanent plot in both primary and logged forests in 1999 and 2002, respectively, to study vegetation, fruit production, and its supra-annual changes. Thanks to the lessons of the other long-term study sites, we realize that, to study social dynamics, we have to systematically monitor changes in the habitat and population simultaneously with group composition and distribution.

Although the long-term study in the coniferous forest is still in its infancy, we found that the macaques are so different from their lowland counterparts in various interesting points. They are much more folivorous: 38 % of their annual feeding time was spent for mature leaves, which was much longer than for fruits (13 %) or seeds (4 %) (Hanya 2004a). Fruit production in the coniferous forest was only one third that of the lowland forest (Hanya et al. 2003a), and most of their main food trees were small-sized, high-density trees (Hanya 2004b, 2009), suggesting that competition is unlikely to occur in the coniferous forest. In fact, intergroup encounters were infrequent in the coniferous forest and not antagonistic when occurring (Hanya et al. 2008). There was no size-dependent difference in birthrate, such as in the lowland forest (Hanya et al. 2008). With respect to the intergroup relationships, the coniferous forest of Yakushima was more similar to Kinkazan, than to coastal forest, although those two forests are only 7 km apart, and there is no genetic differentiation (Hayaishi and Kawamoto 2006). Interestingly, however, female social relationships within a group were quite similar between the coniferous and lowland groups (Hanya et al. 2008). This observation suggests that social behaviors of female Japanese macaques are robust and do not change in response to the current environment.

Another important aspect of Yakushima is that macaque individuals, or even macaque groups, can move between the two study sites. Migration of macaque groups from upward (from east) is observed in the western lowland forest (Sugiura et al. 2002). On the other hand, in the coniferous forest, distribution of the four or five identified groups has been stable for the past 10 years, except the one case of group fission. It is estimated that seven to eight macaque groups are distributed between the two study sites (Yoshihiro et al. 1999), so it may be possible that social dynamics in one of the areas affects the other, at least indirectly. Every summer, similar monitoring of group density, composition, and distribution of multiple identified groups and fruit production is conducted in both these study sites. In the future, Yakushima may offer us a rare opportunity to study the long-term social and population dynamics and within-population interchange of groups in a heterogeneous habitat.

Long-term study of Japanese macaques has revealed a complex and diverse picture of social dynamics. It is now evident that long-term ecological monitoring of the habitat is indispensable to clarify the interrelationships between ecology and society for this species, and we have just started meeting the challenge.

References

Agetsuma N, Nakagawa N (1998) Effects of habitat differences on feeding behaviors of Japanese monkeys: comparison between Yakushima and Kinkazan. Primates 39:275–289

Azuma S (1984) Monkey, forest, and human: a history of biological nature (in Japanese). Monkey 283-285:94–102

Fukuda F (1982) Male movement of transfer between groups of Japanese macaques. Jpn J Ecol 32:491–498

Furuichi T (1985) Inter-male associations in a wild Japanese macaque troop on Yakushima Island, Japan. Primates 26:219–237

Furuya Y (1969) On the fission of troops of Japanese monkeys. II. General view of troop fission of Japanese monkeys. Primates 10:47–69

Hanya G (2002) Island in the southern limit of distribution (in Japanese). In: Oi T, Masui K (eds) Natural history of Japanese macaques: their ecological varieties and conservation. Tokai University Press, Tokyo, pp 229–250

Hanya G (2004a) Diet of a Japanese macaque troop in the coniferous forest of Yakushima. Int J Primatol 25:55–71

Hanya G (2004b) Seasonal variations in the activity budget of Japanese macaques in the coniferous forest of Yakushima: effects of food and temperature. Am J Primatol 63:165–177

Hanya G (2009) Effects of food type and number of feeding sites in a tree on aggression during feeding in wild *Macaca fuscata*. Int J Primatol 30:569–581

Hanya G, Noma N, Agetsuma N (2003a) Altitudinal and seasonal variations in the diet of Japanese macaques in Yakushima. Primates 44:51–59

Hanya G, Yoshihiro S, Zamma K, Kubo R, Takahata Y (2003b) New method to census primate groups: estimating group density of Japanese macaques by point census. Am J Primatol 60:43–56

Hanya G, Matsubara M, Sugiura H, Hayakawa S, Goto S, Tanaka T, Soltis J, Noma N (2004a) Mass mortality of Japanese macaques in a western coastal forest of Yakushima. Ecol Res 19:179–188

Hanya G, Yoshihiro S, Zamma K, Matsubara H, Ohtake M, Kubo R, Noma N, Agetsuma N, Takahata Y (2004b) Environmental determinants of the altitudinal variations in relative group densities of Japanese macaques on Yakushima. Ecol Res 19:485–493

Hanya G, Matsubara M, Hayaishi S, Zamma K, Yoshihiro S, Kanaoka MM, Sugaya S, Kiyono M, Nagai M, Tsuriya Y, Hayakawa S, Suzuki M, Yokota T, Kondo D, Takahata Y (2008) Food conditions, competitive regime, and female social relationships in Japanese macaques: within-population variation on Yakushima. Primates 49:116–125

Hayaishi S, Kawamoto Y (2006) Low genetic diversity and biased distribution of mitochondrial DNA haplotypes in the Japanese macaque (*Macaca fuscata yakui*) on Yakushima Island. Primates 47:158–164

Hill DA, Okayasu N (1995) Absence of youngest ascendancy in the dominance relations of sisters in wild Japanese macaques (*Macaca fuscata yakui*). Behaviour 132:367–379

Izawa K (1988) The ecological study of wild Japanese monkeys living in Kinkazan Island, Miyagi Prefecture: on the population change and the group division (in Japanese). Bull Miyagi Univ Edu 23:1–9

Izawa K (2005) Population changes of Japanese macaques in Kinkazan in 1982–2003 (in Japanese). Miyagiken no Nihonzaru (Jpn Macaques Miyagi Prefect) 19:1–10

Izumiyama S, Mochizuki T, Shiraishi T (2003) Troop size, home range area and seasonal range use of the Japanese macaque in the Northern Japan Alps. Ecol Res 18:465–474

Kawamura S (1958) The matriarchal social order in the Minoo-B Group. Primates 1:149–156

Kimura K, Yoda K (1984) Structure and regeneration process of evergreen conifers and broad-leaved trees in the Yaku-shima Wilderness Area, Yaku-shima. In: Nature Conservation Bureau EA, Japan (ed) Conservation Reports of the Yaku-shima Wilderness Area, Kyushu, Japan. Environment Agency, Tokyo, pp 399–436

Koyama N (1967) On dominance rank and kinship of a wild Japanese monkey troop in Arashiyama. Primates 8:189–216

Koyama N (1970) Changes in dominance rank and division of a wild Japanese monkey troop in Arashiyama. Primates 11:335–390

Kutsukake N, Hasegawa T (2005) Dominance turnover between an alpha and a beta male and dynamics of social relationships in Japanese macaques. Int J Primatol 26:775–800

Maruhashi T (1982) An ecological study of troop fissions of Japanese monkeys (*Macaca fuscata yakui*) on Yakushima Island, Japan. Primates 23:317–337

Maruhashi T (1984) Observe groups through individuals: forest of Yakushima macaques (in Japanese). Monkey 283-285:18–25

Maruhashi T, Saito C, Agetsuma N (1998) Home range structure and inter-group competition for land of Japanese macaques in evergreen and deciduous forests. Primates 39:291–301

Mori A (1979) An experiment on the relation between the feeding speed and the caloric intake through leaf eating in Japanese monkeys. Primates 20:185–195

Nakagawa N, Nakamichi M, Sugiura H (2010) The Japanese macaques. Springer, Tokyo

Oi T (1988) Sociological study on the troop fission of wild Japanese monkeys (*Macaca fuscata yakui*) on Yakushima Island. Primates 29:1–19

Saito C, Sato S, Suzuki S, Sugiura H, Agetsuma N, Takahata Y, Sasaki C, Takahashi H, Tanaka T, Yamagiwa J (1998) Aggressive intergroup encounters in two populations of Japanese macaques (*Macaca fuscata*). Primates 39:303–312

Sprague DS, Suzuki S, Takahashi H, Sato S (1998) Male life history in natural populations of Japanese macaques: migration, dominance rank, and troop participation of males in two habitats. Primates 39:351–363

Sterck EHM, Watts DP, van Schaik CP (1997) The evolution of female social relationships in nonhuman primates. Behav Ecol Sociobiol 41:291–309

Sugiura H, Saito C, Sato S, Agetsuma N, Takahashi H, Tanaka T, Furuichi T, Takahata Y (2000) Variation in intergroup encounters in two populations of Japanese macaques. Int J Primatol 21:519–535

Sugiura H, Agetsuma N, Suzuki S (2002) Troop extinction and female fusion in wild Japanese macaques in Yakushima. Int J Primatol 23:69–84

Sugiyama Y, Ohsawa H (1982a) Population dynamics of Japanese macaques at Ryozenyama: III. Female desertion of the troop. Primates 23:31–44

Sugiyama Y, Ohsawa H (1982b) Population dynamics of Japanese monkeys with special reference to the effect of artificial feeding. Folia Primatol (Basel) 39:238–263

Sugiyama Y, Iwamoto T, Ono Y (1995) Population control of artificially provisioned Japanese monkeys. Primate Res 11:197–207

Suzuki S, Noma N, Izawa K (1998) Inter-annual variation of reproductive parameters and fruit availability in two populations of Japanese macaques. Primates 39:313–324

Tagawa H (1980) Vegetation on the western slope of Mt. Kuniwaridake, Yakushima Island. Sci Rep Kagoshima Univ 29:121–137

Takahashi H, Furuichi T (1998) Comparative study of grooming relationships among wild Japanese macaques in Kinkazan A troop and Yakushima M troop. Primates 39:365–374

Takahata Y, Suzuki S, Okayasu N, Hill D (1994) Troop extinction and fusion in wild Japanese macaques of Yakushima Island, Japan. Am J Primatol 33:317–322

Takahata Y, Suzuki S, Okayasu N, Sugiura H, Takahashi H, Yamagiwa J, Izawa K, Agetsuma N, Hill D, Saito C, Sato S, Tanaka T, Sprague D (1998) Does troop size of wild Japanese macaques influence birth rate and infant mortality in the absence of predators? Primates 39:245–251

Takasaki H, Masui K (1984) Troop composition data of wild Japanese macaques reviewed by multivariate methods. Primates 25:308–318

Yamada M (1963) A study of blood-relationship in the natural society of the Japanese macaque. Primates 4:43–65

Yamagiwa J, Hill D (1998) Intraspecific variation in the social organization of Japanese macaques: past and present scope of field studies in natural habitats. Primates 39:257–273

Yoshihiro S, Furuichi T, Manda M, Ohkubo N, Kinoshita M, Agetsuma N, Azuma S, Matsubara H, Sugiura H, Hill D, Kido E, Kubo R, Matsushima K, Nakajima K, Maruhashi T, Oi T, Sprague D, Tanaka T, Tsukahara T, Takahata Y (1998) The distribution of wild Yakushima macaque (*Macaca fuscata yakui*) troops around the coast of Yakushima Island, Japan. Primate Res 14:179–187

Yoshihiro S, Ohtake M, Matsubara H, Zamma K, Hanya G, Tanimura Y, Kubota H, Kubo R, Arakane T, Hirata T, Furukawa M, Sato A, Takahata Y (1999) Vertical distribution of wild Yakushima macaques (*Macaca fuscata yakui*) in the western area of Yakushima Island, Japan: preliminary report. Primates 40:409–415