

Chapter 1: Research History of Japanese Macaques in Japan

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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 sociometric 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

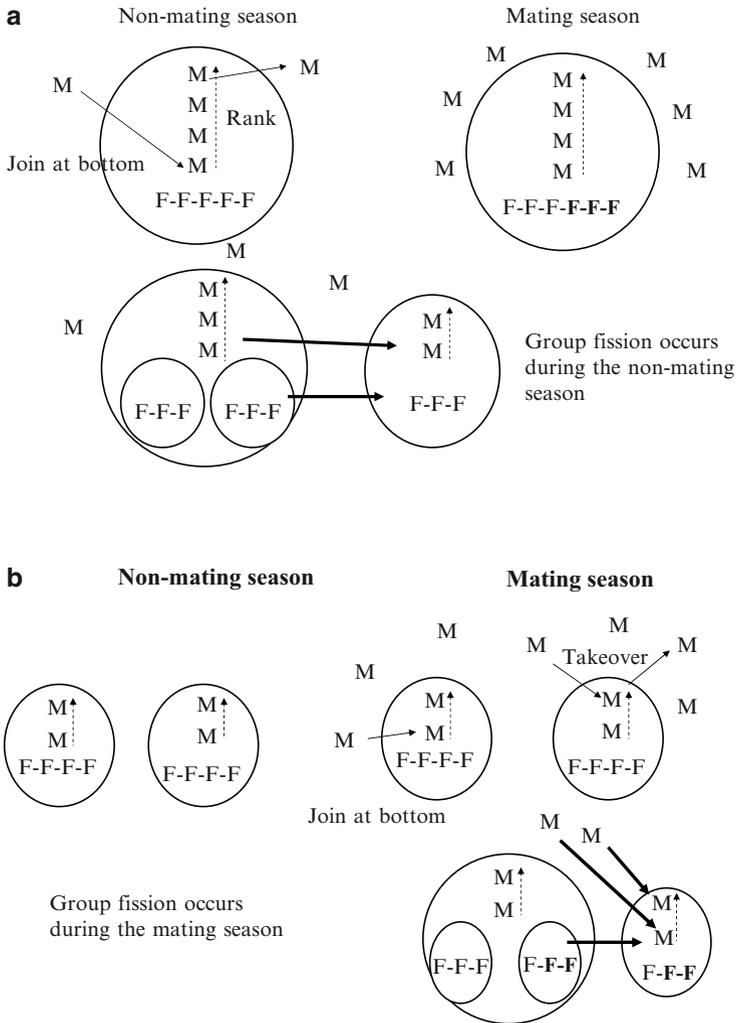


Fig. 1.7 Individual movements and group structure of Japanese macaques based on the studies of provisioned groups (a), and group fissions observed in a population of Yakushima (b). M and F indicate adult male and female macaques, respectively. F An estrous female. Solid arrows, individual movements; 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
<i>Environmental conditions</i>		
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
<i>Ecological features</i>		
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
<i>Reproductive parameters</i>		
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
<i>Social features</i>		
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
<i>Male life history</i>		
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 Yakushima 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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