PRIMATES, 39(3): 257–273, July 1998

Intraspecific Variation in the Social Organization of Japanese Macaques: Past and Present Scope of Field Studies in Natural Habitats

JUICHI YAMAGIWA
Kyoto University
and DAVID A. HILL
University of Sussex

PAST FIELD STUDIES OF JAPANESE MACAQUES IN NATURAL HABITATS

Field studies of Japanese macaques have been conducted for more than 40 years in many parts of the Japanese archipelago. Until the 1970's, the main approach involved habituation of wild macaques using artificial feeding, and identification of each individual to allow records to be made of individual life histories. The main aims of these field studies were to clarify the social structure of Japanese macaques and to identify cultural differences in behavior between populations (IMANISHI, 1952; ITANI, 1954; ITANI & NISHIMURA, 1973). In the early stages of field studies in Japan, therefore, intraspecific variations in social structure and behavior of Japanese macaques were rarely discussed in relation to ecological variation, but were considered rather from the viewpoint of cultural differences (ITANI, 1959, 1963; KAWAI, 1964; KAWAMURA, 1959; TSUMORI, 1967).

In the 1950's and 1960's, Japanese primatologists visited various habitats of Japanese macaques throughout their distribution conducting preliminary surveys (AZUMA, 1966; KAWAMURA & ITANI, 1952; IZAWA, 1962, 1963; NISHIDA, 1966; SUZUKI, 1965; WADA, 1964; YAMADA, 1966; YOSHIBA, 1959). Some evidence of intraspecific variation in aspects of ecology and demography, such as population density, composition of diet, home range size, and group size, were reported during this period. However, after the successful habituation of macaques by provisioning at Koshima, Takasakiyama, Arashiyama, and Minoo in the 1950's, the majority of field studies concentrated on social behavior, as observed in well-habituated macaques at the artificial feeding sites.

By the 1970's, Japanese macaques had been habituated by artificial feeding at more than 30 sites in Japan. Most of these populations were provisioned by cities, prefectures, or travel companies for the purpose of attracting tourists. Heavy provisioning resulted in marked increases in group size, as a result of increased birth rate and decreased infant mortality. Large groups including more than 100 individuals appeared and then fissioned into several groups (SUGIYAMA, 1960; FURUYA, 1960; KOYAMA, 1970). Some important findings, such as permanent residence of females in their natal groups, stability of dominance rank relations within and between female kin-groups, and male emigration from natal groups and transfer between groups, made researchers reconsider their conception of the social organization of Japanese macaques (TOKITA & WADA, 1974; ITOIGAWA, 1975; SUGIYAMA, 1976; NORIKOSHI & KOYAMA, 1975). It became clear that natural populations generally consisted of several groups with partially overlapping home ranges (KAWANAKA, 1973). By contrast, most of the well studied provisioned groups, such as those at Koshima, Takasakiyama, and Arashiyama, were more or less isolated from other groups, and might not, therefore, be representative of a typical local population of Japanese macaques. These findings motivated researchers to study local concentrations of groups living under natural conditions. However, it was not easy to habituate wild macaques without provisioning. In deciduous forests dense undergrowth often prevented researchers from following groups. Most studies were, therefore, conducted in winter, when it was possible to track groups by following footprints left in the snow (IZAWA, 1971, 1982; WADA, 1964, 1981).

In the 1970's and 1980's, road construction and deforestation proliferated throughout Japan and destroyed or degraded much of the natural habitat of Japanese macaques. A decline in agriculture and increased farm mechanization meant that many fields were abandoned and farmers spent less time in those they retained. Abandoned and infrequently tended fields provided wild macaques with their first opportunity to feed on crops and consequently led them to raid fields and orchards beside villages. The struggle between people and macaques increased and in recent years more than 5,000 macaques have been killed or captured annually in pest control programs of local governments in Japan (HILL, 1992; JAPAN PRIMATE NEWS LETTER, No. 3, 1995). At the same time areas of extensive undisturbed natural habitat, in which several groups of Japanese macaques range, have severely decreased during this period.

Kinkazan and the west coast of Yakushima are two areas which escaped the worst of the habitat destruction, and both islands still support areas of relatively undisturbed natural forest. Visibility is also good because both forests are characterized by little undergrowth owing to heavy browsing pressure of deer at Kinkazan, and a closed canopy of warm-temperate evergreen forest in Yakushima. The areas of natural forest at both sites are within National Parks,

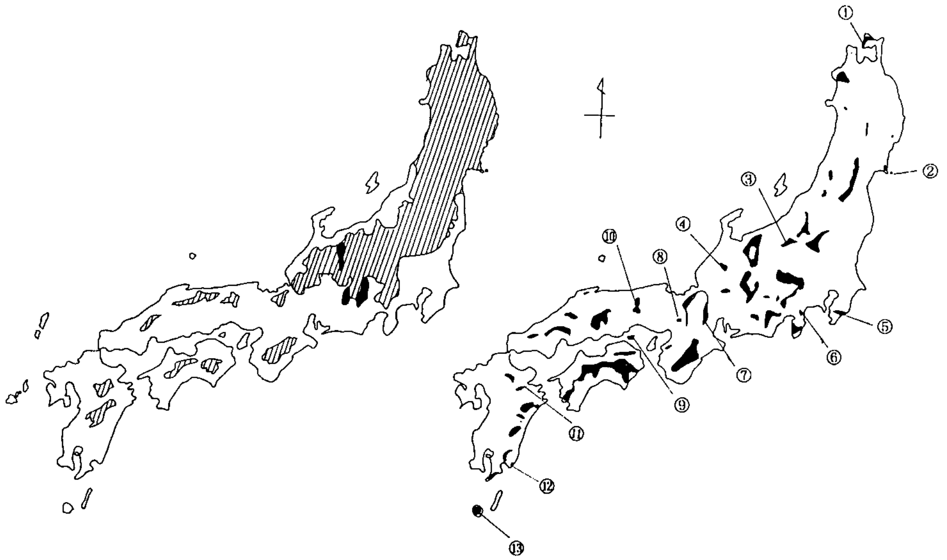

Fig. 1. Map showing the distribution of three types of forest (left) and the distribution of Japanese macaques (right) at the Japan Island. (left) Hatched area: Cool-temperate forest; white area: warm-temperate forest; black area: coniferous forest. (right) Redrawn from UEHARA and KOGANEZAWA (1976). Black area shows the distribution of Japanese macaques: ①Shimokita, ②Kinkazan, ③Shiga Heights, ④Hakusan, ⑤Takagoyama, ⑥Hakone, ⑦Ryozen, ⑧Arashiyama, ⑨Shodoshima, ⑩Katsuyama, ⑪Takasakiyama, ⑫Koshima, ⑬Yakushima.

and there are no human inhabitants (see Preface). After many preliminary surveys, habituation of macaques without artificial feeding was achieved in the mid-1970's in Yakushima and in the early 1980's at Kinkazan. Since then the two areas have attracted many researchers who have studied various aspects of behavior and ecology.

Thus, three types of data are now available for the analysis of the socioecology of Japanese macaques: long-term data on provisioned groups, short-term data on wild unhabituated groups in natural habitats, and long-term data on habituated groups at Kinkazan and Yakushima. Most of the papers presented in this volume aim to elucidate ecological factors influencing the social organization of Japanese macaques by comparing data for Kinkazan and Yakushima. The purpose of this review is to discuss questions posed by the authors against the broader background of findings from other study areas, based on the other two types of data source. We begin by considering the history of field studies on Japanese macaques, and features of social organization which are apparent irrespective of the habitat or provisioning. We go on to examine intraspecific variation and then present a classification of local populations. Finally, we consider priorities for future field research on Japanese macaques.

GENERAL FEATURES OF SOCIAL ORGANIZATION OF JAPANESE MACAQUES

Several features of social organization are common to all groups of Japanese macaques, irrespective of their habitats or provisioning. Japanese macaques form groups consisting of more than two adult males and more than two adult females. The number of groups in a local population fluctuates as a result of increases caused by fission and decreases caused by extinction of groups. The maximum group size recorded is 1,255 individuals at Takasakiyama (SUGIYAMA & OHSAWA, 1988) and the minimum is 3 at Yakushima (TAKAHATA, 1991). The latter group consisted of an adult male, an adult female, and a 4-yr-old female. It eventually became extinct when the male disappeared and the two females joined a neighboring group (MARUHASHI, 1992). This suggests that a group of Japanese macaques may not be maintained with only a single male and small number of females.

Males tend to leave their natal groups before full sexual maturity. Although there are individual variations in age at emigration, maturing males leave their natal groups across a variety of habitats (Toimisaki: AZUMA, 1974; Takasakiyama: MASUI et al., 1974; Katsuyama: ITOIGAWA, 1974; Arashiyama: NORIKOSHI, 1974; Ryozen: SUGIYAMA & OHSAWA, 1974; Yugawara: FUKUDA, 1982; Shiga: TOKITA & WADA, 1974). SPRAGUE et al. (1998) also report that males leave their natal groups around 4 yr old at both Kinkazan and Yakushima. After dispersal from the natal group, a male may spend a period of solitary life, join an all-male group, or transfer directly into another group. He will stay in the new group for several years, but in most cases will leave again and move to another group. It does not seem likely that males return to their natal groups after emigration.

By contrast, females tend to remain in their natal groups throughout their lives, and this sex difference in inter-group movements may result in the avoidance of inbreeding (ITANI, 1972). In most cases, all females within a group will be matrilineal kin. Closely related females associate with each other more than more distant kin, thus forming kin-groups within a group. In this respect, Japanese macaques are regarded as forming 'female-bonded groups' (WRANGHAM, 1980). Group fission occurs between kin-groups in both provisioned and non-provisioned groups (KOYAMA, 1970; OI, 1988; MARUHASHI, 1992). Females persistently associate with females of their own kin-group during and after fission.

Dominance rank among females is linear and stable, and the permanent association of females with kin may enhance this stability. Kinship is clearly not a prerequisite for stability, however, as a stable linear dominance hierarchy is also apparent among males within a group, although the immigrant males have no mature kin in the group (except for the occasional possibility of brothers).

INTRASPECIFIC VARIATIONS

Although a wide range of group sizes have been reported, provisioning has been responsible for all of the larger groups. MASUI (1976) calculated the annual rate of increase in group size at Takasakiyama after provisioning began in 1952 to be 1.102, which means that group size doubled every seven years. Irrespective of location, group size increased after provisioning without exception, and tended to exceed 100 individuals after prolonged (10–20 years) provisioning (NIHONZARU EDITORIAL COMMITTEE, 1977).

By contrast, groups under natural conditions usually fission frequently, and so a relatively small group size is maintained (TAKIZAWA et al., 1994). Mean group sizes calculated for 30 non-provisioned groups are 51.8 (range: 8–166) by MASUI (1976) and 56.4 (range: 10–166) by SUGIYAMA (1985). The mean group size in areas which experience heavy snowfall (33.7, $N=15$, range: 10–79) is smaller than that in areas with lighter snowfall (79.0, $N=15$, range: 17–166) (SUGIYAMA, 1985).

Appendix 1 lists group size, number of adult (older than 5 yr) males and females, and socionomic sex ratio (SSR: number of adult males/number of adult females within a group) for 93 groups in 21 areas. For provisioned groups, data are presented for the same group in different years. Comparing the size of non-provisioned groups between different types of forests, group size in cool-temperate forest and that in Yakushima were not significantly different, however both were significantly smaller than that in warm-temperate forest of areas other than Yakushima (Mann-Whitney U-test, $p<0.01$ and $p<0.001$, respectively, Table 1).

Group size at Kinkazan is intermediate between the heavy and the light snowfall areas. The mean group size at Kinkazan was calculated as 37.2 (range: 25–67, $N=5$) in 1987 (IZAWA & ENDO, 1987), which increased slightly to 41.8 (range: 25–75, $N=6$) in 1995 (SPRAGUE et al., 1998). These results correspond to climatic conditions (neither heavy nor light snowfall) at Kinkazan.

Yakushima is the southern limit of the Japanese macaque's distribution and in the warm temperate forest at low altitudes (0–500 m) there is very little snow. However, the mean group size at Yakushima is very small (32.3, range: 14–57, $N=12$: IWANO, 1983), compared with other areas experiencing light snowfall. The small group size at Yakushima was reported by the earliest studies (KAWAMURA & ITANI, 1952) and is still apparent now, as confirmed in Table 1 and by several papers in this volume.

Table 1. The mean group size and SSR of Japanese macaques in natural habitats.

Forest type	N	Mean group size (range)	Mean SSR (range)
Cool-temperate forest (C)	34	34.9 (8–86)	0.70 (0.3–1.4)
Warm-temperate forest (W)	18	74.8 (17–161)	0.43 (0.1–1.3)
Warm-temperate/subtropical (W/T)	17	27.1 (13–47)	0.79 (0.5–1.0)

Mann-Whitney U-test: group size, C–W, $p<0.01$; W–W/T, $p<0.001$; C–W/T, n.s. SSR, C–W, $p<0.01$; W–W/T, $p<0.001$; C–W/T, n.s.

Evidence from group fissions also suggests marked differences in the maximum group size between different habitats. Under provisioning fission usually occurs, when the group size exceeds 100 individuals (Takagoyama: NISHIDA, 1966; Hagachi, Gagyuzan, and Nametoko: FURUYA, 1969; Ohirayama: KAWAI, 1964; Arashiyama: KOYAMA, 1970; Takasakiyama: SUGIYAMA, 1960), compared with around 70 individuals under natural conditions in Honshu (Hakusan: IZAWA, 1982, 1984; Kinkazan: IZAWA, 1983), and less than 50 individuals in the warm temperate forest of Yakushima (MARUHASHI, 1982, 1992; YAMAGIWA, 1985; OI, 1988).

The difference in the mean or the maximum group size may reflect variations in ecological and social conditions between habitats. TAKASAKI (1981, 1984) proposed a model ($QR=\alpha N$) that correlated troop size (N) and home range area (R) and incorporated a parameter of habitat quality (Q). He showed that the home range area of Japanese macaques was directly proportional to the group size within the same type of forest and that the per capita range area was far larger in deciduous forest than in evergreen forest. As the evergreen forest has more abundant food resources, this suggests that food availability may influence group size quantitatively through its influence on home range area and individual or group density.

As well as group size and home range area, the distribution of food resources may influence relationships between neighboring groups. As MITANI and RODMAN (1979) suggested, defendability, which may depend on home range area and daily path length, may influence territoriality. Data on the home range of Japanese macaques seem to support this hypothesis. In the evergreen forest in Yakushima, the home range of a group was estimated to be 0.87 km^2 (MARUHASHI, 1982). The mean day range of another group, which had the same group size and ranged in the same area as MARUHASHI's study group in subsequent years, was estimated to be 1.02 km ($N=31$, range: 0.8–2.0, YAMAGIWA, unpubl. data). WADA (1981) reported that a group ranged in an area of 2.35 km^2 and traveled 0.65 km per day on average during heavy snow in winter at the Shiga Heights. According to the formula of MITANI and RODMAN (1979), the defendability index (D) for Yakushima (0.97) is close to 1.0 (the limit between territorial and non-territorial) and far higher than that for Shiga Heights (0.38). In fact, groups living in the evergreen forest in Yakushima do show territorial behaviour (MARUHASHI, 1992; MARUHASHI & TAKASAKI, 1996; SAITO et al., 1998), while groups in deciduous forest with heavy snow do not, and occasionally intermingle peacefully with neighboring groups (IZAWA, 1982; WADA, 1981).

The SSR of Japanese macaques varies with group size. The provisioned groups show lower SSR than the non-provisioned groups (Mann-Whitney U-test, $p<0.01$). Among the non-provisioned groups, those inhabiting the warm-temperate forest tend to have lower SSR than those in the cool-temperate forest or those in Yakushima Island (Table 1). The linear regression between group size and SSR is significant for all groups combined ($r=-0.2454$, $p<0.05$) and for the non-provisioned groups ($r=-0.3404$, $p<0.01$). The correlation is not significant for the provisioned groups or for the non-provisioned groups within the same type of forest (cool-temperate forest, warm-temperate forest, and Yakushima Island). These suggest that the SSR may change according to environmental conditions as well as group size. TAKASAKI and MASUI (1984) also reported that SSR tended to decrease under isolated conditions and in artificially disturbed forest. Thus, both social (group size and presence or absence of neighboring groups) and ecological (food conditions) factors may influence SSR.

After emigration from natal groups, male Japanese macaques may spend a period of solitary life, join all-male groups or transfer to other reproductive groups. Which they do varies between habitats. Many solitary males or all-male groups have been observed around large groups with low SSR under isolated conditions at Takasakiyama and Arashiyama (ITANI, 1954; NISHIMURA, 1973; KOYAMA, 1970; NORIKOSHI,1974), while very few solitary males are found around small groups with high SSR in natural populations (MARUHASHI, 1982; IWANO, 1983). Nevertheless, a large number of nonresident males appear around groups during the mating season in Yakushima (YAMAGIWA, 1985; SPRAGUE, 1991a,b, 1992). This is caused by temporary and frequent visiting by resident males to neighboring groups. The small home ranges enable them to visit other groups and to return their own groups within a matter of hours in Yakushima.

The presence of a large group among small groups may also influence the movement of males. At Shiga Heights, a large group appeared after provisioning. Many young males emigrated from this large group and some of them transferred into small neighboring groups (TOKITA & WADA, 1974). On the other hand, few young males appeared around the large group and only adult males transferred into it (WADA, 1979). The emergence of a large group as a result of provisioning may have altered the direction of male's movements.

The seasonality of male movements is also different under different habitat conditions. Among non-provisioned groups, movements are most common during the birth season at Hakone (FUKUDA, 1982), while they are most frequent during the mating season in Yakushima (YAMAGIWA, 1985; SPRAGUE, 1991a,b, 1992). In provisioned groups at Arashiyama, males who become solitary tend to leave their groups at any time in the year, while males transferring into neighboring groups tend to leave groups during the mating season (NORIKOSHI, 1974). In a provisioned group at Shiga Heights, young males first left their natal group for a short time during the mating season and finally left it during subsequent birth and mating seasons (TOKITA & WADA, 1974).

The period of stay by immigrant males at a provisioned group is 4–5 years at Arashiyama (NORIKOSHI, 1974), a maximum of 2 years at Ryozen (SUGIYAMA & OHSAWA, 1974), and a maximum of 5–9 years at Shiga Heights (TOKITA & WADA, 1974). In non-provisioned groups at both Kinkazan and Yakushima, males stay for an average of 2–3 years (SPRAGUE et al., 1998).

A marked difference between provisioned and non-provisioned groups is apparent in the social status of immigrant males. In provisioned groups, immigrant males usually join groups at the lowest dominance rank, while they occasionally join at the top rank in non-provisioned group (YAMAGIWA, 1985; SPRAGUE, 1992; SPRAGUE et al., 1996). Acquisition of the alpha-male rank by immigrant males involves a long process of succession in the provisioned groups, but is sometimes achieved immediately by group take-over or group fission in non-provisioned groups at Yakushima (SPRAGUE et al., 1996). Furthermore, SPRAGUE et al. (1998) report that the immigrant males join at the top rank more frequently at Yakushima (in 13 out of 28 cases) than at Kinkazan (in 1 out 9 cases). These observations suggest that the patterns of associations among resident males within groups may vary not only with food supply (provisioning) but also with group size.

FURUICHI (1983, 1985) reported that agonistic interactions occurred less frequently and affiliative behavior (grooming) among mature males occurred more frequently in a small group at Yakushima than in large provisioned groups in other habitats. HILL (1994) also reported the same tendency in another small group at Yakushima and compared affiliative behavior among males with those of other macaque species. He pointed out that affiliative behavior between adult males was more frequently observed in small groups with a high SSR than in large groups with a low SSR. A shortage of potential grooming partners among the females and their offspring in small groups may stimulate males to choose other males as an alternative. Furthermore, provisioning produces large groups and this may preclude the formation of affiliative relationships among males through increasing levels of aggression and tension (HILL, 1994).

Variation in ecological and social factors may also influence aspects of relationships among females. In large provisioned groups, females acquire their ranks following two principles: (1) a daughter is dominant to all females who are subordinate to her mother (KAWAMURA, 1958, 1965); (2) maturing daughters become dominant to their older sisters, a process which has been termed 'youngest ascendancy' (DATTA, 1988). As a result, females belonging to the same kin-group outrank females of other kin-groups, and dominance rank among mature sisters is inversely correlated with age. By contrast, HILL and OKAYASU (1995) reported the absence of youngest ascendancy in a small group at Yakushima, although in each case the mother was alive and well when the younger sister reached sexual maturity. This runs counter to predictions of models of youngest ascendancy (DATTA, 1989; DATTA & BEAUCHAMP, 1991) and suggests that a different pattern of rank acquisition by female macaques is occurring at Yakushima from that at other sites. HILL and OKAYASU (1996) pointed out that the proximate mechanism by which dominance acquisition takes place is intervention in agonistic encounters, primarily by the mother. They suggested that the highly concentrated resource produced by provisioning increases the need for the mother's role as protector, and might facilitate the process of youngest ascendancy. The occurrence of youngest ascendancy should be examined in relation to the frequency and intensity of aggression between females in non-provisioned groups in other areas.

Group fission tends to occur between kin groups at Yakushima, as observed in the provisioned groups of other habitats (OI, 1988; MARUHASHI, 1992). However, fission is most likely to occur during the mating season at Yakushima, while not in other habitats. YAMAGIWA (1985) reported that the prolonged consort by estrous females and nonresident males caused frequent subgrouping between kin groups and facilitated the process of fission. The weak alliance among resident males and the infrequent support from the mother may cause frequent takeover by outside males or fission reported at Yakushima (YAMAGIWA, 1985; MARUHASHI, 1992; TAKAHATA et al., 1994). The lack of positive support from the mother may reflect relatively loose relationships among females and may contribute to the maintenance of small group size through frequent fissions in Yakushima.

TYPES OF LOCAL POPULATIONS OF JAPANESE MACAQUES

Based on these variations, we can recognize four types of local populations of Japanese macaques (Table 2).

The first type is a local concentration of small groups with small home ranges, such as groups in the warm-temperate forest of Yakushima. They live at high density (individual and group) in a habitat characterized by relatively high quality and abundant food resources (MARUHASHI, 1980; IWANO, 1983; AGETSUMA, 1995a,b). The SSR is close to 1, and solitary males and all-male groups are rarely found. Inter-group relationships are usually antagonistic and territorial, and larger groups are dominant to smaller groups (MARUHASHI, 1982). Emigration or immigration by males is frequent during the mating season (YAMAGIWA, 1985; SPRAGUE, 1991a, 1992). Because temporary visits by males from other groups are frequent during this season, a large number of nonresident males appear around groups, and group fission or takeovers by outside males often occur (YAMAGIWA, 1985; SPRAGUE, 1991a; SPRAGUE et al., 1996; MARUHASHI, 1992). Immigrant males join groups at any social status, although the majority of them join at the bottom or top rank (SPRAGUE et al., 1996). Mature resident males frequently associate with each other and youngest ascendancy is not observed in rank acquisition among females (FURUICHI, 1985; HILL, 1994; HILL & OKAYASU, 1995, 1996).

The second type is a local concentration of medium-size groups with relatively large home ranges, such as groups in the cool-temperate forests of Shimokita, Kinkazan, or Hakusan. They live at low density (individual and group) and utilize relatively scarce, low quality foods, particularly in winter (IZAWA, 1982; NAKAGAWA, 1989a,b; WATANUKI & NAKAYAMA, 1993).

Table 2. Different features of the four types of populations of Japanese macaques.

	Type 1	Type 2	Type 3	Type 4
Population	Yakushima	Hakusan, Shimokita, Kinkazan	Shiga Heights, Hakone, Ryozen	Takasakiyama, Koshima, Arashiyama
Forest type	Warm-temperate	Cool-temperate	Both	Both
Provisioning	No	No	Yes	Yes
Presence of other groups	Yes	Yes	Yes	No
Group density	High	Low	Low	Isolated
Group size	Small	Small to medium	Small to large	Large
Solitary male	Rare	Occasional	Occasional	Frequent
Dominance rank of immigrant male	Various ranks	Mostly bottom rank	Mostly bottom rank	Bottom rank
Emigration of natal male	Before maturity	Before maturity	Some remain after maturity	Some remain after maturity
Seasonality in male's movements	Frequent during mating season	Frequent during mating season	Whole year	Whole year
Seasonality in group fission	Mating season	Mating season	Non-mating season	Non-mating season
Inter-group relation	Territorial	Non-territorial	Non-territorial	

The group size does not exceed 100 individuals and local populations usually include small groups (TAKIZAWA et al., 1994). Group fission occurs at about 70 individuals and is most likely during the mating season (IZAWA, 1984). Inter-group encounters are infrequent and are not antagonistic in many cases (IZAWA, 1982). Territoriality or dominance/subordinate relationships are not apparent between groups (SAITO et al., 1998). Although solitary males and all-male groups are occasionally observed around groups, the number of outside males appearing around groups during the mating season may not exceed the number of resident males (SATO, 1976). Affiliative behavior among mature resident males is infrequent, and the majority of immigrant males join at the bottom rank of the dominance hierarchy (TAKAHASHI & FURUICHI, 1998; SPRAGUE et al., 1998).

The third type is a local concentration of medium-size groups including a large group with relatively large home range, such as groups in the cool-temperate forest at Shiga Heights, and in the warm-temperate forests at Hakone and Ryozen. The large group, which exceeds 100 individuals, is produced by provisioning. In this type of population, male transfer occurs unevenly between groups (FUKUDA, 1988). A large number of young males from the large group transfer into neighboring small groups, while only mature males join the large group. Immigrant males sometimes join small groups at the top rank, while they usually join large groups at bottom rank (HARA, 1971; FUKUDA et al., 1974; TOKITA & WADA, 1974; SUGIYAMA, 1976). Solitary males and all-male groups of various sizes are observed around the large group. In the provisioned group, some males remain in their natal group after reaching maturity, and females occasionally leave to form all-female groups (TOKITA & WADA, 1974; SUGIYAMA & OHSAWA, 1982; FUKUDA, 1983, 1989). Group fission occurs during the non-mating season in large, provisioned groups. Inter-group relationships are not territorial, but large groups are dominant to small groups (WADA, 1979; TOKITA, 1980).

The last type is one or more large, provisioned groups living under isolated conditions, such as those at Takasakiyama, Koshima, and Arashiyama. The field studies of Japanese primatologists were initiated on these populations and the majority of data on social structure and behavior has come from them since provisioning. These groups consist of more than 100 individuals. Since no other groups are found close to them, many males who emigrate from them spend a solitary life or form all-male groups around them (KAWANAKA, 1973; NORIKOSHI, 1974; NISHIMURA, 1977). These non-resident males eventually disperse and may rarely return to their natal groups. Although the number of outside males increases during the mating season, it does not exceed the number of resident males (NISHIMURA, 1977; TAKAHATA, 1980). Some males do not leave their natal groups after maturity (TAKAHATA, 1980). The period of emigration or immigration is not limited to any particular time of year (NORIKOSHI & KOYAMA, 1975). Immigrant males join the group at the bottom of the male dominance hierarchy. Group fission tends to occur during the non-mating season (SUGIYAMA, 1960; NORIKOSHI & KOYAMA, 1975). The ability to maintain close proximity to dominant males or mothers may play an important role in rank acquisition by females at the artificial feeding site (KITAMURA, 1977; TAKAHATA, 1982).

Recently, the habitats of Japanese macaques have been disturbed by deforestation, replacement with conifer plantations (non-food species for Japanese macaques), road construction and cultivation throughout Japan. Macaques are regarded as agricultural pests and have been killed or caught in all prefectures where they survive. Undisturbed natural forests, in which several groups of Japanese macaques range without feeding on artificial foods, are now limited to a few areas, such as Yakushima and Kinkazan. If the former distribution of Japanese macaques consisted of local concentrations of multiple groups (KAWANAKA, 1973), then the populations at Yakushima and Kinkazan may represent this pattern for warm-temperate forest and cool-temperate forest, respectively. Although there are transitional vegetation types between these two, these sites will allow us to study the ecological variables toward the two extremes of the species distribution. The third and fourth population types have both been modified by provisioning or other human disturbances in the recent past.

The papers in this volume examine a range of aspects of social behavior and ecology. AGETSUMA and NAKAGAWA (1998) suggest that the longer feeding time at Kinkazan may be influenced by the larger energy requirement for thermoregulation, and by the fact that food quality is lower than at Yakushima. These differences are responsible for the larger home range and the longer inter-patch distance at Kinkazan (MARUHASHI et al., 1998), where the population consists of larger groups with more highly skewed sex ratios than at Yakushima (SPRAGUE et al., 1998; TAKAHASHI & FURUICHI, 1998). The fact that inter-group encounters are infrequent at Kinkazan may be related to the large home range, while frequent agonistic interactions and inter-group dominance at Yakushima may be related to the clumped distribution of high quality foods. Based on this comparison, SAITO et al. (1998) examined the influence of the cost and benefit of resource defense on inter-group relationships and suggest that antagonism at inter-group encounters may occur in the context of competition for mates between males, rather than the context of resource defense.

TAKAHATA et al. (1998) report that female Japanese macaques of both Kinkazan and Yakushima populations exhibit similar reproductive features. The annual variations in production of fruits during autumn influence the nutritional conditions of Japanese macaques and eventually their birth rate in the following spring (IZAWA, 1990, 1992). SUZUKI et al. (1998) point out that the frequency of inter-group encounters tends to increase during a bad fruiting season, and suggest that the smaller group might suffer from increased inter-group competition at such times. From the results of papers in this volume, it is suggested that clumped food resources may increase inter-group competition which facilitates frequent affiliative interactions between males within groups at Yakushima.

The socioecological approaches in this volume are still at a preliminary stage. It is too early to elucidate the evolutionary processes that led to the social organization or ecology of the Japanese macaques, or to their ability to adapt to the changing environments. The tentative nature of many of the conclusions reflect the need for more data for these two sites. At the same time, the existing data allow us to identify certain priorities for future research. Long-term data are collected by series of fieldworkers whose primary research goals differ. There is clearly a need to co-ordinate the collection of basic data so that the results are directly comparable between research periods and sites. Conservation of these sites must be a major priority to ensure that at least some populations of Japanese macaques continue to thrive in relatively undisturbed conditions. Ideally additional sites should be established between these two, to provide data for conditions between the two extremes. Finally, there is a need to assess the relevance of findings from the many studies of provisioned groups of Japanese macaques. How do provisioning and habitat disruption influence the socioecology of this species, and what implications does this have for populations living under relatively undisturbed conditions?

Acknowledgements. The symposium was financed by the Primate Research Institute Cooperative Research Fund. In writing this review paper we were supported in part by the Monbusho Scientific Research Fund (No. 60166600 to J. YAMAGIWA) and a Collaborative Research Project Grant from the British Council (to D. A. HILL and Prof. H. OHSAWA). We would like to thank Dr. K. IZAWA, Dr. N. NAKAGAWA, Dr. Y. HAMADA, and Dr. D. S. SPRAGUE for co-organizing the symposium with us, and all the participants of the symposium for invaluable help and suggestions.

Appendix 1. Group size and socionomic sex ratio of Japanese macaques reported in various habitats.

Locality (prefecture)		Forest type	Group size	Number**		SSR***	References
				Male	Female		
Shimokita (Aomori)		C	13	4	4	1.0	Izawa & Nishida, 1963
			8	3	4	0.8	〃
			36	5	13	0.4	Izawa et al., 1971
			42	7	18	0.4	〃
			21	8	7	1.1	Swrg, 1985
			11	3	4	0.8	Swrg, 1987
			24	10	7	1.4	〃
Kinkazan (Miyagi)	A	C	53	11	17	0.6	Izawa, 1997
	B1		36	10	11	0.9	〃
	B2		42	11	15	0.7	〃
	C1		31	9	11	0.8	〃
	C2		51	17	15	1.1	〃
	D		79	19	29	0.7	〃
Shiga Heights (Nagano)	1962 A	C	23	7	8	0.9	Suzuki et al., 1975
	1965 A		32*	3	10	0.3	〃
	1970 A		53*	5	18	0.3	〃
	1975 A		95*	8	30	0.3	〃
	B2		19	8	6	1.3	〃
	C		34	11	14	0.8	〃
	1972 B2		24	8	8	1.0	Wada, 1981
Hakusan (Ishikawa)		C	45	9	16	0.6	Kawai et al., 1970
	O		29	3	12	0.3	Izawa, 1972
	KC		39	3	7	0.4	Masui & Ogura, 1972
	IX		31	4	8	0.5	〃
	KMA		101*	7	30	0.2	Takizawa et al., 1995
	KMD		21	2	8	0.3	〃
	TA2-1		71	13	20	0.7	〃
	TA2-2		22	3	5	0.6	〃
	HR		27	3	9	0.3	〃
	OA1		67	10	17	0.6	〃
	OB1		58	7	18	0.4	〃
	OB2		45	13	16	0.8	〃
	KR		86	14	22	0.6	〃
	KNR		27	6	9	0.7	〃
	KNB		19	4	7	0.6	〃
Kurobe (Toyama)		C	20	2	6	0.3	Akaza, 1988
			20	3	7	0.4	〃
			13	3	3	1.0	〃
Takagoyama (Chiba)		W	56	6	15	0.4	Iwano et al., 1971
			109	4	33	0.1	Numata, 1974
Hakone (Kanagawa)		W	46	13	19	0.7	Masui, 1976
			18	3	10	0.3	〃
			134*	28	72	0.4	Fukuda, 1989
Ryozen (Shiga)[a]	1974	W	59*	3	25	0.1	Sugiyama & Ohsawa, 1974
Makino (Shiga)		W	49	5	15	0.3	Nakamichi et al., 1989
			26	4	9	0.4	〃
Hino (Shiga)		W	108	4	31	0.1	Kanazawa et al., 1989
			134	12	49	0.2	〃
			83	12	22	0.5	〃
Arashiyama (Kyoto)	1972 A	W	158*	21	45	0.5	Koyama et al., 1975
	1972 B		143*	19	40	0.5	〃
Minoo (Osaka)		W	86	6	22	0.3	Masui, 1976
			17	1	5	0.3	Kawamura & Kawai, 1956

(continued)

Appendix 1. (continued)

				Number**			
Locality (prefecture)		Forest type	Group size	Male	Female	SSR***	References
Shodoshima (Kagawa)		W	129	48	37	1.3	YAMADA, 1966
			161	17	41	0.4	″
			52	13	17	0.8	″
Gagyusan (Okayama)		W	120	10	35	0.3	FURUYA, 1956
			196*	9	69	0.1	YOSHIHIRO, 1982
Katsuyama (Okayama)	1958	W	112*	13	31	0.4	ITOIGAWA et al., 1992
	1960		143*	13	36	0.4	″
	1965		210*	20	56	0.4	″
	1970		217*	12	53	0.2	″
Taishakukyo (Hiroshima)		W	29	5	9	0.6	MIZUHARA, 1957
Kawaradake (Fukuoka)		W	102	7	33	0.2	EGUCHI, 1970
Takasakiyama (Oita)	1960	W	320*	44	120	0.4	FURUYA, 1960
	1962 A		517*	71	123	0.6	ITANI, 1975
	1962 B		150*	32	23	1.4	″
	1962 C		73*	17	11	1.5	″
	1972 A		890*	90	280	0.3	″
	1972 B		260*	40	65	0.6	″
	1972 C		250*	40	75	0.5	″
Koshima (Miyazaki)	1952	W	22	4	6	0.7	ITANI & TOKUDA, 1958
	1962		52*	11	21	0.5	KAWAI, 1964
Toimisaki (Miyazaki)	1958-59	W	78*	11	20	0.6	AZUMA, 1974
	1960-61		99*	9	23	0.4	″
	1965		170*	16	41	0.4	″
Yakushima (Kagoshima)	To	W/T	27	7	7	1.0	MARUHASHI, 1982
	Ka		13	4	4	1.0	″
	Ha		45	12	12	1.0	″
	Ko		47	12	18	0.7	″
	Ni		25	7	10	0.7	″
	Kw		17	4	6	0.7	″
	Sk		28	8	8	1.0	″
	M#		22	4	6	0.7	YAMAGIWA, 1985
	N#		15	2	3	0.7	″
	A#		27	3	5	0.6	″
	P		18	6	6	1.0	SUGIURA, 1993
	M		28	4	8	0.5	FURUICHI, 1985
	T		17	7	9	0.8	SUZUKI, 1991
	A		38	13	15	0.9	TSUKAHARA, 1990
	H		26	6	10	0.6	TAKAHATA et al., 1994
	NA		46	12	15	0.8	This study
	B		22	5	6	0.8	This study

*Provisioned groups; **number of males and females is calculated for older than 5 years; ***SSR: number of males/number of females. Forest type: C: cool temperate; W: warm temperate; T: subtropical. References: SWRG: Shimokita Wild Animal Research Group, No. groups reformed in 2 years after the Ko group fissioned. a) The group had been provisioned in 1966–1973.

REFERENCES

AGETSUMA, N. 1995a. Dietary selection by Yakushima macaques (*Macaca fuscata yakui*): the influence of food availability and temperature. *Int. J. Primatol.*, 16: 611–627.

AGETSUMA, N. 1995b. Foraging strategies of Yakushima macaques (*Macaca fuscata yakui*). *Int. J. Primatol.*, 16: 595–609.

AGETSUMA, N.; NAKAGAWA, N. 1998. Effects of habitat differences on feeding behaviors of Japanese monkeys: comparison between Yakushima and Kinkazan. *Primates*, 39: 275–289.

AKAZA, H. 1988. Japanese monkeys in the Kurobe Valley. *Monkey*, 216/217: 4–19. (in Japanese)

AZUMA, S. 1966. Distribution of Japanese macaques in Aomori Prefecture, I: Tsugaru eastern Peninsula. *Yaen*, 24: 25–28. (in Japanese)

AZUMA, S. 1974. Formation of dominance rank and emigration in the Toimisaki group. In: *Life History of Male*, WADA, K.; AZUMA, S.; SUGIYAMA, Y. (eds.), Primate Res. Inst., Kyoto Univ., Inuyama, pp. 22–27. (in Japanese)

DATTA, S. B. 1988. The acquisition of dominance among free-ranging rhesus monkey siblings. *Anim. Behav.*, 36: 754–772.

DATTA, S. B. 1989. Demographic influences on dominance structure among female primates. In: *Comparative Socioecology*, STANDEN, V.; FOLEY, R. (eds.), Blackwell Scientific., Oxford, pp. 265–284.

DATTA, S. B.; BEAUCHAMP, G. 1991. Effects of group demography on dominance relationships among female primates: I. Mother-daughter and sister-sister relations. *Amer. Naturalist*, 138: 201–226.

EGUCHI, K. 1970. Capture of Japanese monkeys at Mt. Kawaradake. *Vulpes*, 2 (1): 1–6. (in Japanese)

ENOMOTO, T. 1978. On social preference in sexual behavior of Japanese monkeys (*Macaca fuscata*). *J. Human Evol.*, 7: 283–293.

FUKUDA, F. 1982. Male's movement of transfer between groups of Japanese macaques. *Jap. J. Ecol.*, 32: 491–498. (in Japanese)

FUKUDA, F. 1983. Desertion of female Japanese macaques. *Jap. J. Ecol.*, 33: 347–355. (in Japanese)

FUKUDA, F. 1988. Influence of artificial food supply on population parameters and dispersal in the Hakone T Troop of Japanese macaques. *Primates*, 29: 477–492.

FUKUDA, F. 1989. Habitual fission-fusion and social organization of Hakone troop T of Japanese macaques in Kanagawa Prefecture, Japan. *Int. J. Primatol.*, 10: 419–439.

FUKUDA, F.; MURAMATSU, M.; TANAKA, S. 1974. Inter-troop relationships of wild Japanese macaques at Yugawara. In: *Life History of Male*, WADA, K.; AZUMA, S.; SUGIYAMA, Y. (eds.), Primate Res. Inst., Kyoto Univ., Inuyama, pp. 41–46. (in Japanese)

FURUICHI, T. 1983. Interindividual distance and influence of dominance on feeding in a natural Japanese macaque troop. *Primates*, 24: 445–455.

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

FURUYA, Y. 1956. Natural society of Japanese monkeys at the Mt. Gagyusan. *Res. Rep. Primate Res. Group*. (in Japanese)

FURUYA, Y. 1960. An example of fission of a natural troop of Japanese monkeys at Gagyusan. *Primates*, 2: 149–179.

FURUYA, Y. 1969. On the fission of troops of Japanese monkeys: II. General view of troop fission of Japanese monkeys. *Primates*, 10: 47–69.

HARA, S. 1971. *A Story of Wild Macaques: Taking Bath at Present.* Sinanoji, Nagano. (in Japanese)

HILL, D. A. 1991. Patterns of affiliative relationships involving non-natal males in a troop of wild Japanese macaques (*M. fuscata yakui*) in Yakushima. In: *Primatology Today: Proceedings of the XIIIth Congress of International Primatological Society*, EHARA, A.; KIMURA, T.; TAKENAKA, O.; IWAMOTO, M. (eds.), Elsevier, Amsterdam, pp. 211–214.

HILL, D. A. 1992. Conservation of Japanese macaques (*Macaca fuscata yakui*) in Yakushima: the need for effective protected areas. In: *Topics in Primatology, Vol. 2: Behavior, Ecology, and Conservation*, ITOIGAWA, N.; SUGIYAMA, Y.; SACKETT, G. P.; THOMPSON, R. K. R. (eds.), Univ. of Tokyo Press, Tokyo, pp. 395–401.

HILL, D. A. 1994. Affiliative behavior between adult males of the genus *Macaca*. *Behaviour*, 130: 293–308.

HILL, D. A.; OKAYASU, N. 1995. Absence of 'youngest ascendancy' in the dominance relations of sisters in wild Japanese macaques (*Macaca fuscata yakui*). *Behaviour*, 132: 267–279.

HILL, D. A.; OKAYASU, N. 1996. Determinants of dominance among female macaques: nepotism, demography and danger. In: *Evolution and Ecology of Macaque Societies*, FA, J. E.; LINDBURG, D. G. (eds.), Cambridge Univ. Press, Cambridge, pp. 459–472.

IMANISHI, K. (ed.) 1952. Evolution of humanity. In: *Man*, Mainichi-shinbunsya, Tokyo, pp. 36–94. (in Japanese)

ITANI, J. 1954. *Nihon Dobutsuki, II: The Monkeys of Takasakiyama.* IMANISHI, K. (ed.), Kobunsya, Tokyo. (in Japanese)

ITANI, J. 1959. Paternal care in the wild Japanese monkey, *Macaca fuscata*. *Primates*, 2: 61–93.

ITANI, J. 1963. Vocal communication of the wild Japanese monkey. *Primates*, 4: 11–66.

ITANI, J. 1972. *Social Structure of Primates*. Kyoritsu-shuppan, Tokyo. (in Japanese)

ITANI, J. 1975. Twenty years with Mount Takasaki monkeys. In: *Primate Utilization and Conservation*, BERMANT, G.; LINDBURG, D. G. (eds.), John Wiley & Sons, New York, pp. 101–125.

ITANI, J.; NISHIMURA, A. 1973. The study of infrahuman culture in Japan. In: *Symposia of the Fourth International Congress of Primatology, Vol. 1: Precultural Primate Behavior*, MENZEL, E. W. (ed.), Karger, Basel, pp. 26–55.

ITANI, J.; TOKUDA, K. 1958. *Nihon Dobutsuki, III: Japanese Monkeys on Koshima Island*. IMANISHI, K. (ed.), Kobunsya, Tokyo. (in Japanese)

ITOIGAWA, N. 1974. Emigration of males from the Katsuyama group. In: *Life History of Male*, WADA, K.; AZUMA, S.; SUGIYAMA, Y. (eds.), Primate Res. Inst., Kyoto Univ., Inuyama, pp. 22–27. (in Japanese)

ITOIGAWA, N. 1975. Variables in male leaving a group of Japanese macaques. In: *Proceedings from the Symposia of the Fifth Congress of the International Primatological Society*, KONDO, S.; KAWAI, M.; EHARA, A.; KAWAMURA, S. (eds.), Japan Science Press, Tokyo, pp. 233–245.

ITOIGAWA, N.; TANAKA, T.; UKAI, N.; FUJII, H.; KUROKAWA, T.; KOYAMA, T.; ANDO, A.; WATANABE, Y.; IMAKAWA, S. 1992. Demography and reproductive parameters of a free-ranging group of Japanese macaques (*Macaca fuscata*) at Katsuyama. *Primates*, 33: 49–68.

IWANO, T. 1983. Socioecology of Yakushima macaques (1973–1976). *Nihonzaru*, 5: 86–95. (in Japanese)

IZAWA, K. 1962. Japanese monkeys at Kinkazan. *Monkey*, 60: 6–8. (in Japanese)

IZAWA, K. 1963. Seeking for monkeys in northern areas, II: Feeding habits of Japanese monkeys in Shimokita Peninsula. *Monkey*, 70: 14–16. (in Japanese)

IZAWA, K. 1971. Japanese monkeys living in the Okoppe basin of the Shimokita Peninsula: the first report of the winter follow-up survey after the aerial spraying of herbicide. *Primates*, 12: 191–200.

IZAWA, K. 1972. Ecological survey of wild Japanese monkeys living in Hakusan National Park: (1) Group nomadism and intergroup relationships in the snowy season. In: *Scientific Studies of Hakusan National Park in 1971*, JINKAI, H. C. K. (ed.), Ishikawaken, pp. 6–18. (in Japanese)

IZAWA, K. 1982. *Ecology of Japanese Monkeys*. Dobutsusha, Tokyo. (in Japanese)

IZAWA, K. 1983. The ecological study of wild Japanese monkeys living in Kinkazan Island, Miyagi Prefecture. *Bull. Miyagi Univ. Educ.*, 18: 24–46. (in Japanese)

IZAWA, K. 1984. Troop fission of wild Japanese macaques in the Hakusan area and its ecological meaning. *Res. Rep. Hakusan Conserv. Ctr.*, 10: 99–110. (in Japanese)

IZAWA, K. 1990. The ecological study of wild Japanese monkeys living in Kinkazan Island, Miyagi Prefecture: on the change of birth rate and infant mortality. *Bull. Miyagi Univ. Educ.*, 25: 177–191. (in Japanese)

IZAWA, K. 1992. The ecological study of wild Japanese monkeys living in Kinkazan Island, Miyagi Prefecture: on the change of birth rate and infant mortality (a supplement). *Bull. Miyagi Univ. Educ.*, 27: 69–75. (in Japanese)

IZAWA, K. 1997. Population census of Japanese macaques at Kinkazan in 1996. In: *The Japanese Macaques in Miyagi Prefecture, Vol. 9*, Miyagi Primate Res. Group, Miyagi, pp. 1–14. (in Japanese)

IZAWA, K.; ENDO, J. 1987. Distribution and folk customs of Japanese macaques according to questionnaire. In: *The Japanese Macaques in Miyagi Prefecture, Vol. 2*, Miyagi Primate Res. Group, Miyagi, pp. 1–12. (in Japanese)

IZAWA, K.; IMAI, K.; TANAHASHI, A. 1971. Do the monkeys living in the northern limit survive during the winter?: research report in winter after dealing herbicide 1. *Monkey*, 117: 6–11. (in Japanese)

IZAWA, K.; NISHIDA, T. 1963. Monkeys living in the northern limit of their distribution. *Primates*, 4 (2): 67–88.

JAPAN PRIMATE NEWSLETTER, NO. 3. 1995. Committee of Conservation and Animal Welfare, Primate Society of Japan.

KANAZAWA, T.; NAKAMICHI, M.; SHIMIZU, S.; IMAGAWA, S.; MACHIDA, S.; TAKEDA, S.; SAKAI, A.; ITOIGAWA, N. 1989. Troops of wild Japanese macaques living in Hino town, Shiga Prefecture. In: *Research Report of Wild Japanese Macaques in Shiga Prefecture*, Lab. Comp. Psychol., Faculty of Human Sci., Osaka Univ., Osaka, pp. 25–27.

KAWAI, M. 1964. *Ecology of Japanese Monkeys*. Kawadeshobo, Tokyo. (in Japanese)

KAWAI, M.; AZUMA, S.; YOSHIBA, K.; HAYASHI, K.; TAKESHITA, H.; MIZUHARA, H.; IZAWA, K. 1970. Ecological studies of Japanese monkeys around the Hakusan 1. In: *Scientific Studies of Hakusan National Park, Japan*, Ishikawa Prefecture, Ishikawa, pp. 335–343. (in Japanese)

KAWAMURA, S. 1958. The matriarchal social order in the Minoo-B group: a study on the rank system of Japanese macaque. *Primates*, 1: 149–156. (in Japanese with English summary)

Kawamura, S. 1959. The process of sub-culture propagation among Japanese macaques. *Primates*, 2: 43–60.

Kawamura, S. 1965. Matriarchal social ranks in the Minoo-B troop: a study of the rank system of the Japanese monkeys. In: *Japanese Monkeys*, Imanishi, K.; Altmann, S. A. (eds.), Chicago, pp. 105–112.

Kawamura, S.; Itani, J. 1952. *Natural Society of Yakushima Macaques*. Primate Res. Group of Kyoto Univ., Kyoto. (in Japanese)

Kawamura, S.; Kawai, M. 1956. Social organization of the natural group of Japanese macaques: the case of the Minoo-B group. *Nihon Seitai Gakkai-shi*, 6: 45–50. (in Japanese with English summary)

Kawanaka, K. 1973. Intertroop relationships among Japanese monkeys. *Primates*, 14: 113–159.

Kitamura, K. 1977. Special proximity relations between individuals in Japanese monkeys. *Kikan Jinruigaku* (*Quarterly Anthropol.*), 8: 3–39. (in Japanese)

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

Maruhashi, T. 1980. Feeding behavior and diet of the Japanese monkey (*Macaca fuscata yakui*) on Yakushima Island, Japan. *Primates*, 21: 141–160.

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. 1992. Fission, takeover, and extinction of a troop of Japanese monkeys (*Macaca fuscata yakui*) on Yakushima Island, Japan. In: *Topics in Primatology, Vol. 2*, Itoigawa, N.; Sugiyama, Y.; Sackett, G. P.; Thompson, R. K. R. (eds.), Univ. of Tokyo Press, Tokyo, pp. 47–56.

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.

Maruhashi, T.; Takasaki, H. 1996. Socio-ecological dynamics of Japanese macaque troop ranging. In: *Evolution and Ecology of Macaque Societies*, Fa, J. E.; Lindburg, D. G. (eds.), Cambridge Univ. Press, Cambridge, pp. 146–159.

Masui, K. 1976. A record on group size and composition of Japanese macaques: reconsideration on the knowledge of group size and population. *Ecol. Physiol.*, 17: 185–194. (in Japanese)

Masui, K.; Ogura, S. 1972. Research report on wild Japanese monkeys around Jadani Valley. In: *Hakusan Research on Resource 1971*, Hakusan Res. Committee (ed.), Ishikawaken, pp. 19–23.

Masui, K.; Sugiyama, Y.; Nishimura, A.; Ohsawa, H. 1974. Life table of Japanese macaques at Takasakiyama. In: *Life History of Male*, Wada, K.; Azuma, S.; Sugiyama, Y. (eds.), Primate Res. Inst., Kyoto Univ., Inuyama, pp. 47–54. (in Japanese)

Mitani, J. C.; Rodman, P. S. 1979. Territoriality: the relation of ranging pattern and home range size to defendability, with an analysis of territoriality among primate species. *Behav. Ecol. Sociobiol.*, 5: 241–251.

Mizuhara, H. 1957. *Japanese Monkeys*. Sanichi-shobo, Kyoto. (in Japanese)

Nakagawa, N. 1989a. Bioenergetics of Japanese monkeys (*Macaca fuscata*) on Kinkazan Island during winter. *Primates*, 30: 441–460.

Nakagawa, N. 1989b. Feeding strategies of Japanese monkeys against deterioration of habitat quality. *Primates*, 30: 1–16.

Nakamichi, M.; Kanazawa, T.; Imagawa, S.; Takeda, S.; Shimizu, S.; Sakai, A.; Itoigawa, N. 1989. Troops of wild Japanese macaques living in Makino town, Shiga Prefecture. In: *Research Report of Wild Japanese Macaques in Shiga Prefecture*, Lab. Comp. Psychol., Faculty of Human Sci., Osaka Univ., Osaka, pp. 4–7.

Nihonzaru Editorial Committee. 1977. Change in population of Japanese macaques at Monkey Parks in Japan. *Nihonzaru*, 3: 113–120. (in Japanese)

Nishida, T. 1966. A sociological study of solitary male monkeys. *Primates*, 7: 141–204.

Nishimura, A. 1973. The third fission of a Japanese monkey group at Takasakiyama. In: *Behavioural Regulators of Behaviour in Primates*, Carpenter, C. R. (ed.), Bucknell Univ. Press, Lewisburg, pp. 115–123.

Nishimura, A. 1977. Troop fission at Takasakiyama: from the third fission to the sixth fission. In: *Research Report of Japanese Monkeys at Takasakiyama 1971–76*, Ohita City, Ohita, pp. 37–91. (in Japanese)

Norikoshi, K. 1974. Mother-infant relationships in the natural group of Japanese macaques. *Kikan Jinruigaku*, 5 (2): 39–62. (in Japanese)

Norikoshi, K.; Koyama, N. 1975. Group shifting and social organization among Japanese monkeys. In: *Proceedings from the Symposia of the Fifth Congress of the International Primatological Society*, Kondo, S.; Kawai, M.; Ehara, A.; Kawamura, S. (eds.), Japan Science Press, Tokyo, pp. 43–61.

NUMATA, M. 1974. Research report on habitat of Japanese monkeys: a natural treasure at the Mt. Takagoyama. Educational Committee of Chiba Prefecture, Chiba. (in Japanese)

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.

SATO, S. 1976. Male bond in matrilineal groups: reconsideration on social structure of Japanese macaques. *Res. Rep. Hakusan Conserv. Ctr.*, 3: 75–93. (in Japanese)

SPRAGUE, D. S. 1991a. Influence of mating on the troop choice of non-troop males among Japanese macaques of Yakushima Island. In: *Primatology Today*, EHARA, A.; KIMURA, T.; TAKENAKA, O.; IWAMOTO, M. (eds.), Elsevier Science, Amsterdam, pp. 207–210.

SPRAGUE, D. S. 1991b. Mating by non-troop males among the Japanese macaques of Yakushima Island. *Folia Primatol.*, 57: 156–158.

SPRAGUE, D. S. 1992. Life history and male intertroop mobility among Japanese macaques (*Macaca fuscata*). *Int. J. Primatol.*, 13: 437–454.

SPRAGUE, D. S.; 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.

SPRAGUE, D. S.; SUZUKI, S.; TSUKAHARA, T. 1996. Variation in social mechanisms by which males attained the alpha rank among Japanese macaques. In: *Evolution and Ecology of Macaque Societies*, FA, J. E.; LINDBURG, D. G. (eds.), Academic Press, London, pp. 444–458.

SUGIURA, H. 1993. Temporal and acoustic correlates in vocal exchange of coo calls in Japanese macaques. *Behaviour*, 124: 207–225.

SUGIYAMA, Y. 1960. On the division of a natural troop of Japanese monkeys at Takasakiyama. *Primates*, 2: 109–148.

SUGIYAMA, Y. 1976. Life history of male Japanese monkeys. *Adv. Stud. Behav.*, 7: 255–284.

SUGIYAMA, Y. 1985. Ecology of Japanese macaques. In: *Introduction of Primatology*, EHARA, A.; OHSAWA, W.; KAWAI, M.; KONDO, S. (eds.), Iwanami Press, Tokyo, pp. 298–315. (in Japanese)

SUGIYAMA, Y.; OHSAWA, H. 1974. Population dynamics of Japanese macaques at Mt. Ryozen. In: *Life History of Male*, WADA, K.; AZUMA, S.; SUGIYAMA, Y. (eds.), Primate Res. Inst., Kyoto Univ., Inuyama, pp. 55–62.

SUGIYAMA, Y.; OHSAWA, H. 1982. Population dynamics of Japanese macaques at Ryozenyama III: female desertion of the troop. *Primates*, 23: 31–44.

SUGIYAMA, Y.; OHSAWA, H. 1988. Population dynamics and management of baited Japanese monkeys at Takasakiyama. *Primate Res.*, 4: 33–43. (in Japanese with English summary)

SUZUKI, A. 1965. An ecological study of Japanese monkeys in snowy areas: focused on their food habits. *Primates*, 6: 31–72.

SUZUKI, A.; WADA, K.; YOSHIHIRO, S.; TOKITA, E.; HARA, S.; ABURADA, Y. 1975. Population dynamics and group movement of Japanese monkeys in Yokoyugawa valley, Shiga Heights. *Physiol. Ecol.*, 16 (1): 15–23. (in Japanese)

SUZUKI, S. 1991. Dominance relationships of young males in a troop of Japanese monkeys in Yakushima, Japan. In: *Primatology Today*, EHARA, A.; KIMURA, T.; TAKENAKA, O.; IWAMOTO, M. (eds.), Elsevier Science, Amsterdam, pp. 133–136.

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.

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. 1980. The reproductive biology of a free-ranging troop of Japanese monkeys. *Primates*, 21: 303–329.

TAKAHATA, Y. 1982. Social relations between adult males and females of Japanese monkeys in the Arashiyama B troop. *Primates*, 23: 1–23.

TAKAHATA, Y. 1991. Social interactions in a small-sized troop of wild Japanese monkeys in Yakushima Island, Japan. In: *Primatology Today*, EHARA, A.; KIMURA, T.; TAKENAKA, O.; IWAMOTO, M. (eds.), Elsevier Science, Amsterdam, pp. 101–104.

TAKAHATA, Y.; SUZUKI, S.; OKAYASU, N.; HILL, D. A. 1994. Troop extinction and fusion in wild Japanese monkeys of Yakushima Island, Japan. *Amer. J. Primatol.*, 33: 317–322.

TAKAHATA, Y.; SUZUKI, S.; AGETSUMA, N.; OKAYASU, N.; SUGIURA, H.; TAKAHASHI, H.; YAMAGIWA, J.; IZAWA, K.; FURUICHI, T.; HILL, D. A.; MARUHASHI, T.; SAITO, C.; SATO, S.; SPRAGUE, D. S. 1998. Reproduction of wild Japanese macaque females of Yakushima and Kinkazan Islands: a preliminary report. *Primates*, 39: 339–349.

TAKASAKI, H. 1981. Troop size, habitat quality and home range area in Japanese macaques. *Behav. Ecol. Sociobiol.*, 19: 277–281.

TAKASAKI, H. 1984. A model for relating troop size and home range area in a primate species. *Primates*, 25: 22–27.

TAKASAKI, H.; MASUI, K. 1984. Troop composition data of wild Japanese macaques reviewed by multivariate methods. *Primates*, 25: 308–318.

TAKIZAWA, H.; IZAWA, K.; SHITAKA, K. 1994. On the change in group sizes and home ranges of Japanese monkeys living in Mt. Hakusan area, Ishikawa Prefecture VIII. *Res. Rep. Hakusan Conserv. Ctr.*, 21: 27–42. (in Japanese with English summary)

TAKIZAWA, H.; IZAWA, K.; SHITAKA, K. 1995. On the change in group sizes and home ranges of Japanese monkeys living in the Mt. Hakusan area, Ishikawa Prefecture IX. *Res. Rep. Hakusan Conserv. Ctr.*, 22: 19–27. (in Japanese with English summary)

TOKITA, E. 1980. Fission of Shiga-A troop of Japanese macaques. *Anim. Nature*, 10: 26–30. (in Japanese)

TOKITA, E.; WADA, K. 1974. The process of male emigration and immigration in Shiga-A group. In: *Life History of Male*, WADA, K.; AZUMA, S.; SUGIYAMA, Y. (eds.), Primate Res. Inst., Kyoto Univ., Inuyama, pp. 28–34. (in Japanese)

TSUKAHARA, T. 1990. Initiation and solicitation in male-female grooming in a wild Japanese macaque troop on Yakushima Island. *Primates*, 31: 147–156.

TSUMORI, A. 1967. Newly acquired behavior and social interactions of Japanese monkeys. In: *Social Communication Among Primates*, ALTMANN, S. A. (ed.), Univ. of Chicago Press, Chicago, pp. 207–219.

UEHARA, S.; KOGANEZAWA, M. 1976. Historical change in the distribution of Japanese macaques. *Kagaku*, 46 (12): 737–744. (in Japanese)

WADA, K. 1964. Ecology of Japanese monkeys in the snowy area: life and inter-troop relationships of B troop in winter at Shiga Height. *Yaen*, 16/17: 14–17. (in Japanese)

WADA, K. 1979. *World of Wild Japanese Monkey*. Kodansha, Tokyo. (in Japanese)

WADA, K. 1981. Habitat utilization by wintering Japanese monkeys (*Macaca fuscata fuscata*) in the Shiga Height. *Primates*, 22: 330–348.

WATANUKI, Y.; NAKAYAMA, Y. 1993. Age difference in activity pattern of Japanese monkeys: effects of temperature, snow, and diet. *Primates*, 34: 419–430.

WRANGHAM, R. W. 1980. An ecological model of female-bonded primate groups. *Behaviour*, 75: 262–300.

YAMADA, M. 1966. Five natural troops of Japanese monkeys in Shodoshima Island I: distribution and social organization. *Primates*, 7: 315–362.

YAMAGIWA, J. 1985. Socio-sexual factors of troop fission in wild Japanese monkeys (*Macaca fuscata yakui*) on Yakushima Island, Japan. *Primates*, 26: 105–120.

YOSHIBA, K. 1959. Research report of wild Japanese macaques in Tohoku Region. *Yaen*, 5: 15–23. (in Japanese)

YOSHIHIRO, S. 1982. Japanese monkeys at Gagyusan. *Bull. Hiruzen Res. Inst., Okayama Univ. of Sci.*, 7: 61–80. (in Japanese)

—— Received: *November 25, 1996*; Accepted: *November 22, 1997*

Authors' Names and Present Addresses: JUICHI YAMAGIWA, *Faculty of Sciences, Kyoto University, Oiwake-cho, Kitashirakawa, Sakyo-ku, Kyoto City, Kyoto 606-8502, Japan*; DAVID A. HILL, *School of Biological Sciences, University of Sussex, Falmer, Brighton, East Sussex, BN1 9QG, England.*