PRIMATES, 29(4): 477–492, October 1988

Influence of Artificial Food Supply on Population Parameters and Dispersal in the Hakone T Troop of Japanese Macaques

FUMIO FUKUDA

ABSTRACT. A free-ranging troop of Japanese monkeys was observed for seven years from April 1971 to March 1978 in the Hakone area, Kanagawa Prefecture, Japan. This troop was fed artificially between 1956 and 1977. The artificial food supply was reduced by about half after 1974. The troop-size fluctuated around 100 between 1971 and 1974, but fell drastically from 91 in 1975 to 58 in 1978. Population parameters were compared between the two periods of 1971–1974 and 1975–1977. Clear differences between the two periods were found in primiparous age, ratio of non-natal resident males to all resident males, ratio of newcomers to non-natal resident males, age-specific disappearance rate, and proportion of deserters observed in the study area. A correlation existed between the number of males and females of 5 or more years of age in the troop. The numbers in the three age-sex groups (natal males, non-natal males, and females of 5 or more years of age in the troop) were closely connected with one another. The scarcity of food supply may have caused not only males but also females to disperse. The drastic decrease in troop-size after 1974 could be based on the disappearance of adult females. The cause of the dispersal of young males and adult females could have been mutual competition among the troop members for food, and that in adult males could have been competition for females.

Key Words: *Macaca fuscata*; Artificial food supply; Population parameter; Non-natal male; Dispersal.

INTRODUCTION

The relationship between the population parameters and dominance rank order of macaques (genus *Macaca*) has been studied by many workers. The birth rate of high-ranking females is higher than that of low-ranking females, and the survival rate of infants of the former is higher than that of infants of the latter (DRICKAMER, 1974). Moreover, the daughters of high-ranking females reproduce at an earlier age than those of low-ranking females (DRICKAMER, 1974; DITTUS, 1979; MORI, 1979) and high-ranking mothers are more likely to give birth to daughters than sons (SIMPSON & SIMPSON, 1982). High-ranking females tend to copulate with high-ranking males (SAMUELS et al., 1984). However, SILK et al. (1981), GOUZOULES et al. (1982), WOLFE (1984), and NIEUWENHUIJSEN et al. (1985) argued that the dominance rank of females was not significantly correlated with reproduction. On the other hand, MORI (1979) and SUGIYAMA and OHSAWA (1982) reported that artificial feeding influenced the population parameters of the troop. Artificial feeding increases the birth rate, lowers the infant mortality, and hastens the primiparous age, especially of high-ranking kin. However, reports on the relationship between artificial food supply and population parameters which include dispersal in Japanese monkeys (*Macaca fuscata*) are few.

I describe here the population dynamics of the Hakone T troop with special references to the changes in artificial food supply. The relation between population parameters including dispersal and artificial food supply is discussed.

MATERIALS

Hakone is a recreational area that has been designated as a national park since 1936. Consequently, the wild life in the area has been conserved and several troops of Japanese

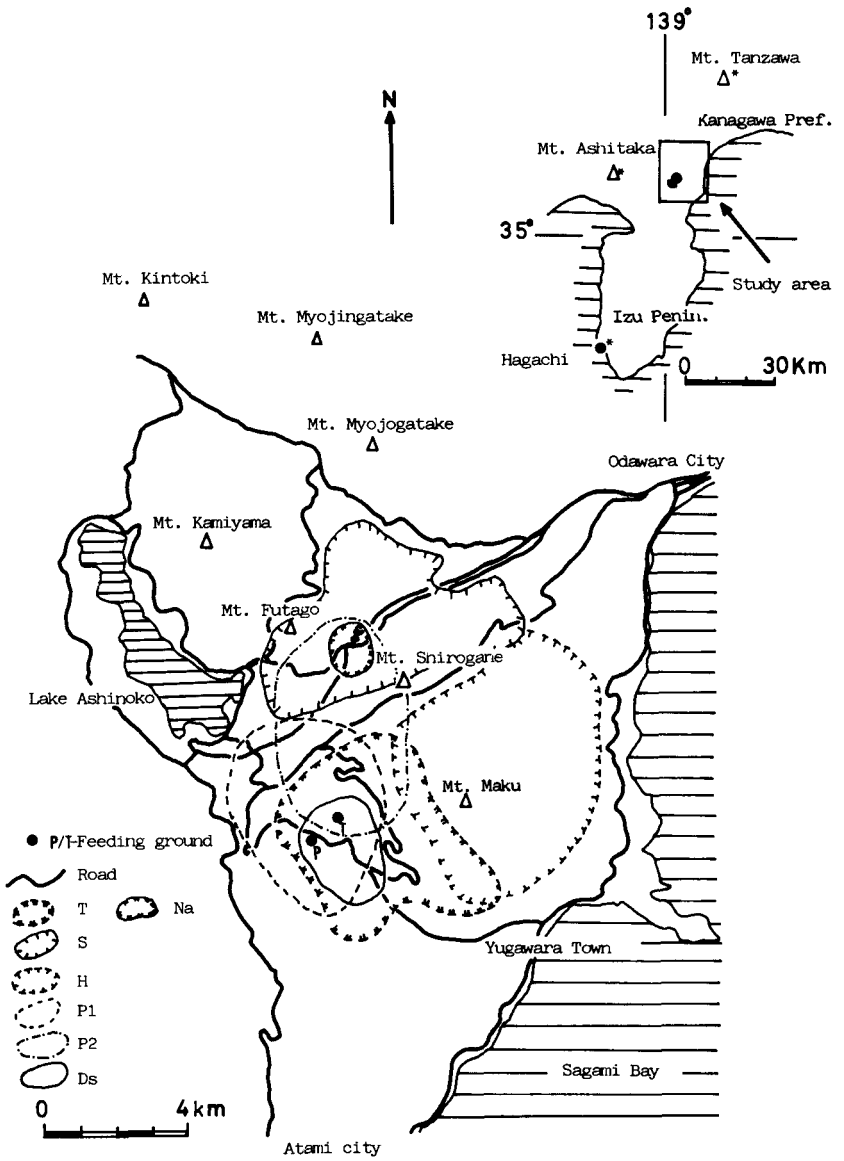

Fig. 1. Ranges of seven troops in the Hakone mountains between January 1975 and December 1977. The locations of three other populations close to the Hakone mountains are indicated by asterisks in the inset (upper right).

monkeys inhabit the southeastern slopes of Mt. Shirogane to Mt. Maku (Fig. 1). The area is covered by secondary forests containing evergreen broad-leaved trees (*Osmanthus ilicifolius, Litsea aciculata, Benzoin umbellatum*, etc.) and deciduous broad-leaved trees (*Alnus japonica, Cornus controversa, Wistaria floribunda*, etc.). Plantations of *Cryptomeria japonica* exist in places and sight-seeing drive-ways have been built, by which the ranging of monkey troops has often suffered disturbance. Slopes near the eastern coast are partially occupied by tangerine orchards.

The study troop (Hakone T troop) was fed artificially at the T feeding site by the Yugawara town office between 1956 and September 1977. The troop-size was said to be about 35 in 1956 (the late Mr. S. KAMIZAWA, pers. comm.). A keeper visited the feeding site almost every day and, when monkeys appeared, threw wheat and sweet potatoes on the ground (ca. 25 × 40 m). The feeding site was located near the center of the troop's range, which measured about 16 km^2 (January 1975 to December 1977; see also Fig. 1). Other troops (P and S) were identified in the area. The P troop was fed artificially at the P feeding site by a motorbus company between 1964 and September 1974. In November 1974, the P troop fissioned into the P1 and P2 troops. Both consisted of about 20 animals in March 1978. The S troop was identified on the north slopes of Mt. Shirogane from 1969, and was sometimes fed artificially in the winter from 1969 to 1975. This troop consisted of about 20 animals in May 1979, when animals derived from the T troop and P troop were often identified. Some new troops were formed by animals including females who came from adjacent troops. The newly-formed troops, after 1966 when my observations began, were as follows. The H troop was formed by two adult males from the P troop, three adult females from the T troop and seven others in 1967. This troop sometimes visited the T and P feeding sites until 1970. Subsequently, its range expanded to the northeastern area of the present day. The troop-size in May 1976 was about 40. The I troop fissioned from the T troop in December 1972 (11 adult females, 8 adolescent males, 4 adult males, 5 juveniles, and 2 infants). The animals from the T troop (excluding two adult females, one adolescent male and one juvenile) returned to the T troop before March 1973 and this troop collapsed. Such temporary troop-fission of the study troop in winter (January–March) also occurred twice during January–March 1975 and 1977. The Na troop was formed by two adult females, which deserted the T troop one by one, two unknown adult females, and four adult males in January 1976. This troop ranged in the northern area which was included in the range of the S troop, and then joined with the P2 troop in January 1978 (FUKUDA, 1983). The Ds troop was formed by four adult females, which deserted the T troop one by one in 1975, and one adult male in February 1976. Subsequently, another two adult females which deserted the T troop between November 1977 and April 1978 joined the Ds troop, although two other females disappeared from the Ds troop. The Ds troop foraged in a small area near the T and P feeding sites and its size in May 1979 was five.

In the neighborhood of the Hakone area, monkey troops inhabit the central and southern part of the Izu peninsula, the Tanzawa mountains, and Mt. Ashitaka (Fig. 1). Three tattooed young males which left their natal T troop were found alive in the Hagachi troop, which is located about 60 km to the south of the T feeding site (FUKUDA, 1982).

Feral dogs probably represented the only predator in the area (MIYAKI, 1976). Tourists sometimes fed the monkeys along the roads which run through the ranges of the troops. As a result, some monkeys must have been killed in traffic accidents (once per one to three years). Monkeys sometimes raided the tangerine orchards during the winter, so that some of them were captured (five from the H troop in July 1971 and ten from the P1 troop in April 1978)

or shot (two each in the T troop in February 1973 and September 1977, and five in the H troop between July 1978 and January 1979). More detailed information has been reported by BURTON and FUKUDA (1981) and FUKUDA (1982, 1983).

METHODS

The above troops were observed continuously from May 1966. However, this paper focuses on observations of the T troop covering 723 days from April 1971 to March 1978. The animals of the study troop, as well as those of the P (P1 and P2), Na, and Ds troops and some animals of the H and S troops, have been identified since May 1966. Some were identified with the use of hair dye (mainly infants) and tattoos on their faces. Demographic records, such as the membership of the troops, births, disappearances, and shifting of animals among the troops, were continuously recorded throughout the study period by me and several other co-researchers. The ages of the animals up to 4 years were readily discerned because clear differences existed between these age classes. Since observations had continued from 1966, the ages of most animals up to 9 years old in the troop in 1971 were known. The older animals could be roughly divided into four age classes: 10–14, 15–19, 20–24, and 25 or more years old. All 32 females who were at least 4 years old in the T troop in 1966 were defined as matriarchs of the kin-groups, including three 3-year-old juveniles whose mothers were not known. Animals which were identified in the troop in 1966 were treated as natals. [Among the males which were at least 5 years old in 1966, two still remained in the troop until April 1971, and these were included among the non-natal animals since most Japanese male monkeys are known to leave their natal troops in their youth (SUGIYAMA, 1976)]. *Non-natal animals* in this paper means animals which came from other troops and foraged with high-ranking males and females of the T troop for one or more months. *Newcomer animals* means non-natal animals which were seen in the T troop for the first time. *Residents* means 5- and more than 5-year-old natal and non-natal animals which were seen in the T troop from the previous year. *Disappearances* means animals which disappeared from the T troop and never returned to it again, i.e., including animals which deserted, were killed, captured, or were dead or alive but not found. *Deserters* means animals which were found alive after disappearance, except for those captured.

Since births were concentrated in the period from April to October, the ages of the animals were arbitrarily counted on the basis of April. A year in this paper means from April to the next March, unless otherwise noted. The data on the amounts of artificial food supply depended on the records of the T feeding site. The calories of artificial food supply (wheat, 348 Cal/100 g; sweet potatoes, 123 Cal/100 g) were based on MATSUMOTO (1985).

RESULTS

CHANGES IN SIZE OF THE T TROOP

The population changes in the study troop from 1956 to 1978 are illustrated in Figure 2 together with the separation of small troops. The figure shows the troop-sizes in April of the respective years, except 1966 when the troop-size was counted in May. During the first 11 years, artificial feeding was continued, and the size of the study troop nearly doubled; that is, from about 35 in 1956 to 69 in 1966 when my observations started. The size continued to in-

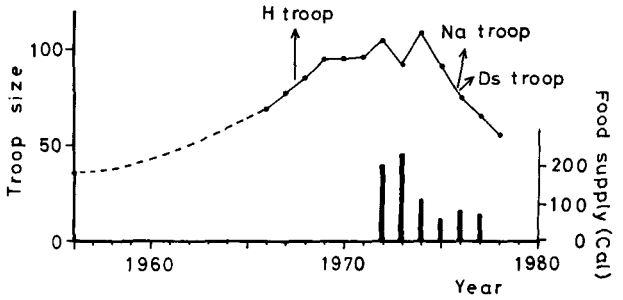

Fig. 2. Changes of T troop-size and artificial food supply, and new troops separating from the troop. Food supply is shown as the amount per capita per diem.

crease until 1969 (95 animals). However, between 1969 and 1974, the size fluctuated around 100. Then, between 1974 and 1978, the size fell drastically to 57 animals. Thus, these 13 years between 1966 and 1978 can be classified into three periods: an increasing period before 1968, a fluctuating period between 1969 and 1974, and a decreasing period from 1975.

The artificial food supply per capita per diem during 1972–1977 is also shown in Figure 2. The average food supply in 1972 and 1973 was about 200 Cal, that in 1974 decreased to 122 Cal, while after 1975 it decreased to less than half the original amount (to about 70 Cal). According to a public officer of the Yugawara town office, the annual amount of food supply before 1971 appeared to be the same as that in 1972. The drastic decrease in troop-size began in 1974, when the food supply was decreased to almost half that of the previous year.

Births and Infant Mortality

During the seven years between April 1971 and March 1978, 149 births were recorded and, among them, 75 (50.3%) of the infants (less than 1 year old) disappeared (Table 1). The annual birth rate (number of births/number of females of at least 5 years old) varied from 34% (in 1972) to 83% (in 1971). The low birth rate in 1972 could have been caused in part by the high birth rate of the preceding year, while the capturing which was carried out in March, just before the birth season, could possibly have caused some miscarriages or still-births. The mean birth rate for 1971–1974 (56.9%) was slightly higher than that for 1975–

Table 1. Birth rate, infant mortality, and primiparous age.

Year	No. of adult females[1)]	Primiparous age (in years)	No. of births				Birth rate	Disappeared[2)]				Infant mortality
			Male	Female	?	Total		Male	Female	?	Total	
1971	36	5, 5, 5, 6, 6, 7	14	11	5	30	83.3	6	5	5	16	53.3
1972	41	5	8	5	1	14	34.1	4	3	1	8	57.1
1973	42	6, 6, 6, 6, 7	10	14	1	25	59.5	1	5	1	7	28.0
1974	48	5, 6, 6, 7	10	13	3	26	54.2	6	8	3	17	65.4
1975	40	6	9	9	—	18	45.0	2	6 (1)	—	8 (1)	38.9
1976	33	7, 7, 7, 8	5	7	2	14	42.4	2	4	2	8	57.1
1977	31	6, 7, 7, 8	10	10	2	22	71.0	4	5	2	11	50.0
Total	271	$N = 25$	66	69	14	149	55.0	25	36 (1)	14	75 (1)	49.7

1) Five or more than 5 years old; 2) number of infants which disappeared from their birth-dates to next March.
( ): Deserted with her mother.

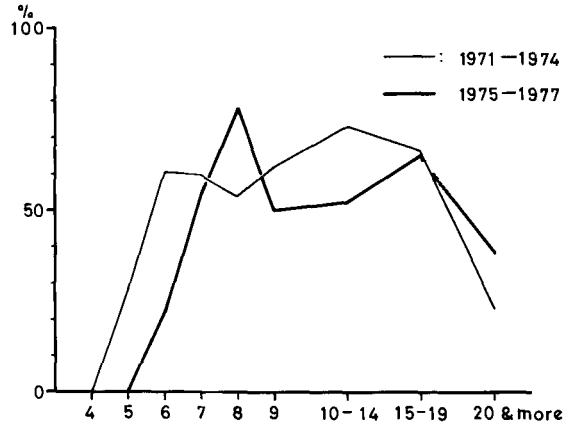

Fig. 3. Age-specific birth rate with reference to two study periods.

1977 (51.9%). However, there was no significant difference between the two periods. Twenty-five females gave birth to their first infants during the seven-years. The primiparous age varied from 5 to 8 years old. The mean primiparous age before 1974 ($M = 5.9 \pm 0.7$, $N = 16$) was significantly younger than that after 1975 ($M = 7.0 \pm 0.7$, $N = 9$) (median test, $\chi^2 = 6.287$, $df = 1$, $p < 0.02$). Thus, the primiparous age in the decreasing period, when the artificial food supply decreased, was about 1 year older than that in the fluctuating period when there was as much as about twice the food supply. The artificial food supply, without doubt, strongly influenced the primiparous age.

The age-specific birth rates of the fluctuating (1971–1974) and decreasing (1975–1977) periods were compared (Fig. 3). The age-specific birth rates in 1971–1974 were higher than those in 1975–1977, except for the age 8 years and age 20 or older groups. The reason why the birth rate of the age 8 year groups in 1975–1977 was higher than that in 1971–1974 could be the retardation of the primiparous age after 1975. The reason why the birth rate of the age 20 or older females in 1975–1977 was higher than that in 1971–1974 must have been the existence of extremely old females who rarely delivered offspring but still remained in the troop only during the fluctuating period. Consequently, the birth rate in 1971–1974 was reduced by the presence of senile females. The decreased food supply after 1975 thus appears to have influenced more the primiparous age of young females than the birth rate of older females.

The sex ratio (female/male) at birth was 1.045, which did not differ significantly from 1.000 (Table 1). There was no significant difference in sex ratio between the fluctuating and decreasing periods. However, when the mother's age was classified into three classes, the infant

Table 2. Number of infants of both sexes at birth by three age-classes of mothers in 1971–1974 and 1975–1977.

	Age-class (in years)							
	5–9		10–14		15 & more		Total	
	Male	Female	Male	Female	Male	Female	Male	Female
1971–1974	16	16	14	11	12	16	42	43
1975–1977	11	9	9	3	4	14	24	26
Total	27	25	23	14	16	30	66	69

sex ratio was significantly different among those classes, as follows: 0.926 for age 5–9 years mothers (52 infants), 0.609 for age 10–14 years mothers (37 infants), and 1.875 for age 15 or older mothers (46 infants) ($\chi^2 = 7.129$, $df = 2$, $p<0.05$). The oldest females tended to give birth to more females than males ($\chi^2 = 4.260$, $df = 1$, $p<0.05$). This tendency was more conspicuous in the decreasing period than in the fluctuating period (Table 2). However, the cause of the trend remains unknown.

The birth seasons during 1971–1977 were recorded. Among all births ($N = 149$), 82.6% ($N = 123$) were from May to July. The median birth dates in 1971–1974 and 1975–1977 were the same (June 15). However, births in the decreasing period were more concentrated in May–July (48/54, 88.9%) than those in the fluctuating period (75/95, 78.9%), although no significant difference was found. There is a possibility that abundant food supply could expand the sexual activity and then the birth season.

Infants depend on their mothers and cannot survive alone. The infants that disappeared were never found alive again, except for one female infant which deserted the troop with its mother. The disappearance of infants was regarded as death, from which the infant mortality was calculated (Table 1). Among 149 infants which were born during 1971–1977, 74 (49.7%, excluding the one female which deserted with its mother) disappeared before the next April. Fourteen disappeared before their sex was confirmed. The annual infant mortality varied from 28% (in 1973) to 65% (in 1974) (no significant difference was found among the seven-years). The infant mortality in 1971–1974 when artificial food supply was abundant was 0.51, and that in 1975–1977 when the artificial food supply was scarce was 0.48. No significant difference was found between the infant mortalities of the two periods. The infant mortality of the study troop was very high compared with those of other troops (in the artificial feeding period, Koshima = 0.149 and Ryozenyama = 0.18; in the restricted feeding period, Koshima = 0.688 and Ryozenyama = 0.30) (MORI, 1979; SUGIYAMA & OHSAWA, 1982). The artificial feeding of the Koshima and Ryozenyama troops must have influenced the nutrient condition of the infants and their mothers and lowered the infant mortality. On the other hand, the high mortality of the study troop through the study period might possibly have been based on the habitual fission-fusion of the troop: even mothers and their infants were sometimes found in different subgroups (FUKUDA et al., 1974; FUKUDA, in prep.). For this reason, accidental deaths of infants may have obscured the difference between the two periods. The mortality of female infants was significantly higher than that of male infants in each year (Wilcoxon's signed rank test, $N = 7$, $T = 5$, $p<0.02$), but no difference was observed between the fluctuating and decreasing periods. Similarly, DITTUS (1979) reported that female infant mortality was higher than that for males among toque monkeys (*M. sinica*).

Out of 105 infants born from 1973 to 1977, 51 (48.6%) disappeared before the following April. The monthly distribution of infant disappearance is illustrated in Figure 4. Eighteen (35.3%) disappeared from November to December, while 12 (23.5%) disappeared from July to August. The number of disappearances in November–December was significantly greater than that in other months ($\chi^2 = 15.564$, $df = 1$, $p<0.001$), but that in July–August was not significantly greater. Thus, the infant losses were somewhat concentrated within a few months of birth in the first half of the mating season. The infant losses from November to December may have been caused by heightened levels of aggression of the males (KOFORD, 1965; DRICKAMER, 1974; WILSON & BOELKINS, 1970), desertions of their mothers from the troop (FUKUDA, 1983) and predation by feral dogs (MIYAKI, 1976). The infant losses in July–August, just after the median birth dates, could have been deaths of infants in poor health,

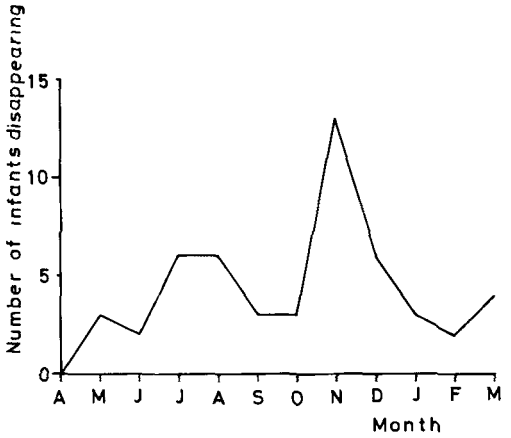

Fig. 4. Monthly distribution of infant disappearances from the T troop between April 1973 and March 1978 ($N = 51$).

although there was no significant difference in July–August between the fluctuating and decreasing periods.

Non-natal ANIMALS

During the seven-years between April 1971 and March 1978, 49 *non-natal* males and 2 *non-natal* females were observed in the study troop, and another 6 *non-natal* males were known to have been in it before the study period (Table 3). Out of the 55 *non-natal* males, 19 (34.5%) came from adjacent troops: P = 14, Pl = 1, H = 3, and S = 1. Most of the *non-natal* males were at least 5 years old ($N = 51$, 92.7%), and all of the young males of 4 or less than 4 years old ($N = 4$) originated in adjacent troops. Concerning the age of the *newcomer* males when they were first seen in the study troop, age 5- to 6- and 10- to 11-year-old males were most common. Younger males, of less than 9 years old, tended to stay continuously for more than three years, while about half of the at least 9-year-old males tended to repeat leaving and joining the T troop for more than one year. Such leaving and joining

Table 3. Residents, newcomers, disappearances, and amount of artificial food supply.

Year	Troop size	Residents			Newcomers		Disappearances					Food supply (Cal per capita per diem)
		Male		Female	Male	Female	Male		Female			
		N	Non				N	Non	N	Non	Total[1)]	
1971	96	6	6	36	6 (2)	—	12 (10)	1	9 (8)	—	27 (23)	
1972	105	6	11 (1)	41	11	—	15 (11)	11	10 (7)	—	37 (19)	197
1973	93	4	11	42	6	—	6 (4)	2	6 (6)	—	15 (11)	228
1974	109	4	15	48	16 (1)	2	15 (14)	14 (1)	28 (18)	2	62 (36)	112
1975	91	4	17	40	5	—	13 (11)	9	18 (10)	—	40 (21)	57
1976	74	2	13	33	4 (1)	—	7 (6)	8 (1)	10 (7)	—	27 (16)	83
1977	65	2	9	31	1	—	6 (5)	3	17 (8)	—	29 (15)	74
Total	633	28	82 (1)	271	49 (4)	2	74 (61)	48 (2)	98 (64)	2	237 (141)	

1) Including infants whose sex was unknown (see Table 1). Figures in parentheses indicate animals of 4 and less than 4 years old. N: Natal animals; Non: non-natal animals (see Methods).

males, when they were not seen in the subject troop, were usually found in the adjacent troops (FUKUDA, 1982). Thus, 10 to 31 *non-natal* males were always observed in the troop each year, comprising more than 80% of the males of age 5 or older in the troop. The number of *newcomers* which were observed in the troop for the first time varied from 1 (in 1977) to 16 (in 1974).

Among the *resident* males in the troop, the number of *non-natal* males exceeded that of *natal* males through the seven-years (Table 3). The ratio of *non-natal* males to all *resident* males during 1971–1974 was significantly lower than that during 1975–1977 (Mann-Whitney test, $U = 0$, $p<0.05$). On the other hand, among all *non-natal* males, the ratio of *newcomers* during 1971–1974 was significantly higher than that during 1975–1977 ($U = 0$, $p<0.05$). The shortage of artificial food supply during 1975–1977 could have caused the number of *newcomers* to decrease, and the ratio of *non-natal* males to all *resident* males to increase. This suggests that the food shortage might have encouraged *natal* males to desert from the study troop, while *non-natal resident* males could remain in the troop. One factor which may encourage dispersal from the *natal* troop by males could be related to the amount of food. However, the dispersal of *non-natal* males must also be based on factors other than food. These problems will be discussed in a later section.

In contrast to the *non-natal* males, two *non-natal* females were seen separately in the troop during January to March 1975. They were observed in the troop for only 1.5 months and 2 months, respectively. One returned to her original troop (P2) and the other, whose original troop was unknown, disappeared with the collapse of the subgroup of the T troop which formed during January to March 1975 (FUKUDA, 1983).

Among the troop animals including *residents* and *newcomers* of at least 5 years of age, there was a significant correlation between the number of males and females in each year (correlation coefficient test, $r = 0.922$, $N = 7$, $df = 5$, $p<0.005$), irrespective of the amount of artificial food supply (Table 3). The existence of such a correlation suggests that the number of males which were at least 5 years old was affected by the number of females which were at least 5 years old, the number of *non-natal* or *natal* males was also affected by the number of females, and the numbers of the three age-sex groups were closely connected with one another.

DISAPPEARANCE FROM THE TROOP AND SURVIVORSHIP

The number of animals which disappeared from the T troop during the study period is shown in Table 3. The disappearing animals included 123 males (49 non-natals and 74 natals) and 100 females (2 non-natals and 98 natals). Out of the natal animals, 85.1% ($N = 63$) of the males and 65.3% ($N = 64$) of the females disappeared before the age of 5 years. Thirteen (32.5%) of the natal males, which disappeared at 2 and more than 2 years old, were found again in adjacent troops (P = 10, P2 = 1, H = 1, and S = 1) about five months later, while males which disappeared before they reached the age of 2 years were never found alive again ($N = 34$). Three tattooed natal males (including two which disappeared from the troop in August 1969 and August 1980) were found in the Hagachi troop, about 60 km south from the T feeding ground, after one year or more (FUKUDA, 1982).

Fifty percent ($N = 17$) of the disappearing females of at least 5 years of age were found again living in the Hakone area, while females which disappeared before 5 years old were never found again alive ($N = 64$), except for three females which deserted with their mothers.

Table 4. Number of deserters* in all disappearances in 1971–1974 and 1975–1977.

	Deserters		Disappearances		Rate[1)] of deserters	
	Males	Females	Males	Females	Males	Females
1971–1974	10	8	26	14	0.38	0.57
1975–1977	3	9	14	20	0.21	0.45
Total	13	17	40	34	0.325	0.50

*Animals which were found alive in the Hakone area. 1) Rate of deserters in terms of the disappearances. Males: 2 and more than 2 years old; females: 5 and more than 5 years old.

Most deserting females of at least 5 years of age were matriarchs ($N = 10$) of their kin-groups, and the eldest daughters ($N = 6$) of the matriarchs. Three deserted with their offspring and 14 alone. Most female deserters tended to derive from lower-ranking kin-groups in the troop [for details, see FUKUDA (1983)]. Most female deserters (except for four females) disappeared from the Hakone area within three years after they were found alive. Probably, some of them were not dead, but had dispersed to other areas outside Hakone, because after troop desertion some of them were able to enter easily into other troops, form new troops with other female deserters, pair with an adult male, forage alone or forage with their infants (FUKUDA, 1983). Most males which disappeared after the age of 2 years, and some of the females which disappeared after the age of 5 years, were probably alive, while most younger males and females were presumed to have died.

Table 4 lists the numbers of natal animals found alive in the Hakone area after they had disappeared from the T troop. The percentages of deserters found with respect to all disappearances in both sexes in 1971–1974 were higher than those in 1975–1977 (however, there was no significant difference between the periods for either sex). This suggests that the scanty food supply may have induced animals to disperse to distant areas other than adjacent troops in the Hakone area, although there is no concrete evidence. This problem will be discussed in a later section.

The number of disappearing animals was correlated with the artificial food supply. In a year when the food decreased, more animals disappeared; while in a year when the food increased, less animals disappeared (Spearman's rank correlation test, $r_s = 1.00$, $N = 5$, $p<0.01$) (Table 3).

Figure 5 shows the age-specific disappearance rates for natal animals of the T troop in 1971–1974 and 1975–1977. Concerning the males, the disappearance rates revealed similar tendencies in both periods. The disappearance rate of 4-year-olds rose markedly in both periods. The rate for 3- to 6-year-old males in 1975–1977 was higher than that in 1971–1974. Similarly, the disappearance rate of females in 1975–1977 was significantly higher than that in 1971–1974 (Wilcoxon's signed rank test, $T = 14$, $p<0.04$). In particular, about 40% of the 15- to 19-year-old females disappeared in 1975–1977, and the rate was remarkably high as against the rate of the same age class in 1971–1974, which was about 4%. The reduction in the artificial food supply could have influenced the disappearance rate of both sexes. Especially, it may have caused 3- to 6-year-old males and older females to accelerate their disappearance from the troop. Accordingly, the drastic decrease in troop-size after 1974 was not based on a low birth rate and high infant mortality, but on troop-desertions and disappearances of adult females.

The number of juvenile natal males decreased rapidly up to the age of 5 years in both peri-

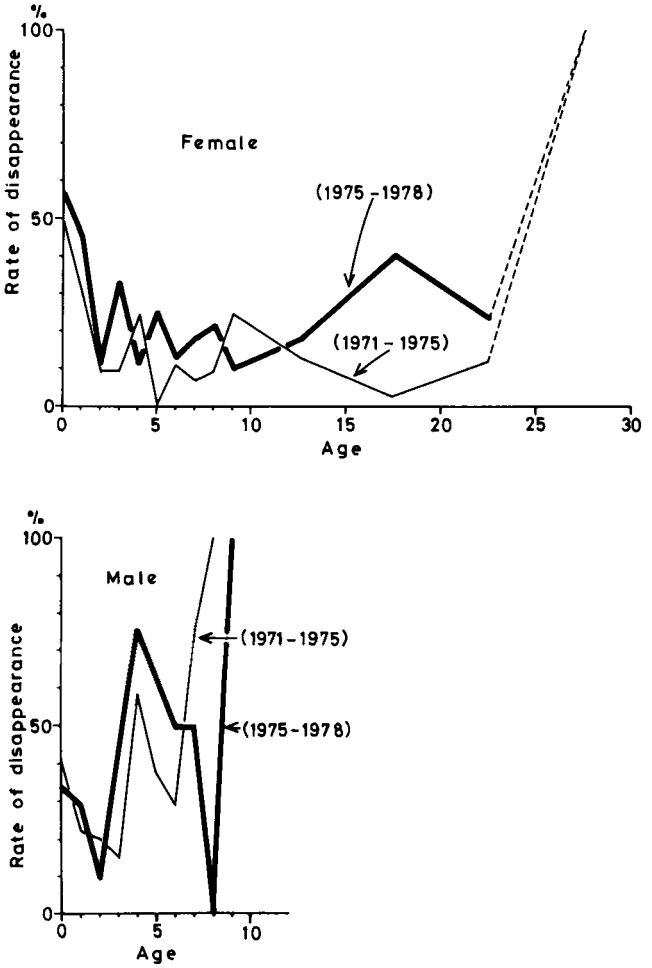

Fig. 5. Age-specific disappearance rate (the proportion of animals disappearing per 100 entering each age class).

ods, 1971–1974 and 1975–1977 (Fig. 6). By two years after birth, the number of natal males decreased to less than half, and at 5 years old it decreased to less than 10% of births. All natal males disappeared before the age of 10 years. Natal females decreased more rapidly than natal males until the age of 2 years, and at 5 years old only about 20% of animals born remained. The decrease rate of females after the age of 5 years was rather slow. Thus, the food shortage during 1975–1977 reduced the natal female remaining rates in the troop. The influence of food shortage on the male remaining rate was not so clear as that in females, perhaps because of the strong tendency of males to leave the natal troop.

DISCUSSION

Artificial food supply can influence various population parameters, such as primiparous

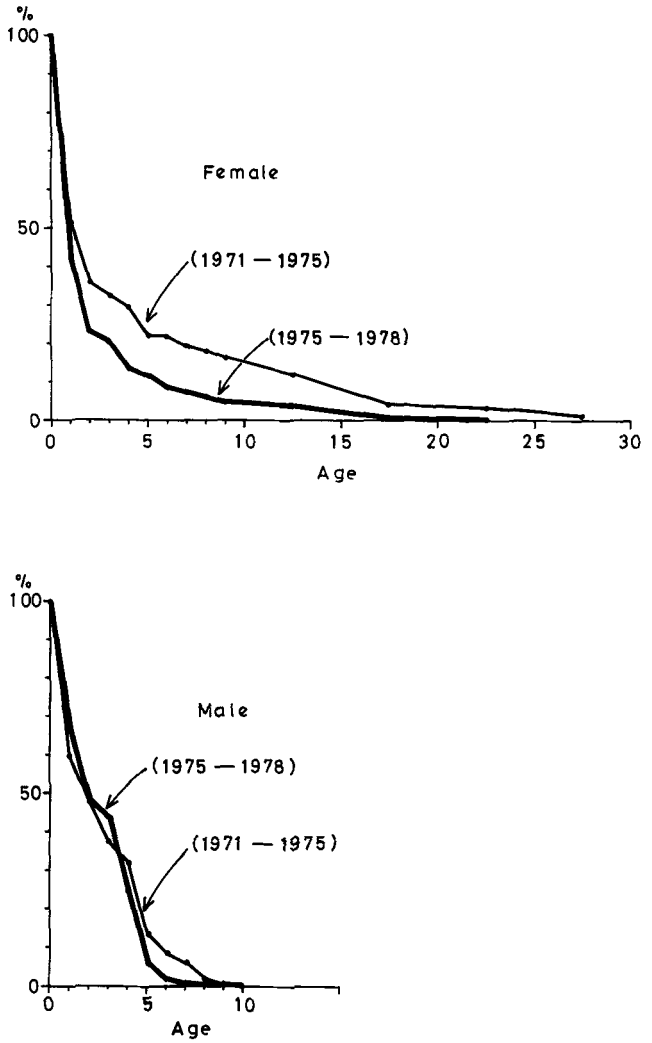

Fig. 6. Cumulative percentage of natal animals remaining in the T troop.

age, birth rate, infant mortality, etc. (MORI, 1979; SUGIYAMA & OHSAWA, 1982). The present study confirmed the above conclusion for primiparous age and birth rate, but the infant mortality was not influenced by the artificial food supply, while the results also showed that the number of newcomer males and dispersal of natal males could be affected by artificial food supply. Moreover, decrease in the artificial food supply influenced more the disappearance of females than of males from the study troop. MOORE and ALI (1984) argued that dispersal from the natal group or area in birds and mammals is not for the purpose of inbreeding avoidance but because of intrasexual competition, and the key factors in the competition differ between the sexes. Female Japanese monkeys do not usually leave their natal troop. However, in other troops as well as the study troop in which troop desertion by females has been found, many female desertions occurred after artificial feeding stopped

(Ryozenyama; SUGIYAMA & OHSAWA, 1982) or when the amount of food supply was severely restricted (Koshima; MORI, 1979). In the present study troop, the age-specific disappearance rate of females in the scarce food supply period was significantly higher than that in the abundant food supply period, and a significant correlation was observed between the amount of food supply and the number of female disappearances (FUKUDA, 1983). Moreover, low-ranking females tended to desert more than high-ranking ones (FUKUDA, 1983). These findings suggest that females of the study troop competed with each other for food when the food supply became scarce. Accordingly, when females disperse, one of the key factors which causes them to disperse could be a scarcity of food. On the other hand, it seems that key differences existed between young and adult males, rather than between natal and non-natal males. As shown in Figure 5, the disappearance rate between the ages of 3 to 6 years in the scarce food supply period was higher than that in the abundant food supply period. The main factor involved in young males of under 5 years could thus be competition for food, which may accelerate their dispersal from the natal troop. The key factor for adult males of age 5 or older could be competition among the adult males for adult females. When the food supply decreased, the number of natal males of at least 5 years old which remained in the troop was few, and the number of newcomer males was also few. Therefore, because the competition for adult females among the resident males in the scanty food supply period was less severe than that in the abundant food supply period, the non-natal resident males must easily have remained within the troop. The correlation between the number of males and females of age 5 or older could support these hypotheses.

The natal males of age 2 or more which disappeared from the study troop in the scarce food supply period were rarely found in the adjacent troops, compared with those in the abundant food supply period (Table 4). This might be based on any of the following three possibilities: (1) many of the males which disappeared died during the food shortage; (2) many disappearing males were alive in the Hakone area, but were not found; and (3) many disappearing males dispersed to distant areas other than Hakone. Concerning (1), there was no influence of the food supply shortage on the infant mortality, although the food supply shortage would be expected to affect this most (MORI, 1979; SUGIYAMA & OHSAWA, 1982). Accordingly, it seems doubtful whether many of the natal male disappearances in the scarce food supply period were due to death. Concerning (2), many animals of the adjacent troops or solitary animals were accustomed to being fed by tourists along the many roads. Thus, if T troop males were in fact in the Hakone area, they probably would have been found. Accordingly, (2) seems doubtful also. Concerning (3), the artificial feeding of the P and S troops was stopped in 1974 and 1975, respectively. Consequently, the shortage of artificial food supply of the troops in the Hakone area began from 1974. All the natal male deserters until 1975 were found in the P troop where artificial feeding was carried out every day. However, none were found in other adjacent troops (S and H) where artificial feeding was limited or was not carried out. Moreover, after the artificial feeding of the P troop was stopped, natal male deserters were found to be only one in the P (P1 and P2) troop. This resembles the pattern seen in the T troop, where the numbers of newcomer males in the abundant food supply period were greater than those in the scarce food supply period. Therefore, some natal male disappearances in the scarce food supply period did not approach the adjacent troops because of the scarce food supply of the adjacent troops, but dispersed to distant areas where food supply may have been abundant.

Females disappeared from the T troop with decrease in the artificial food supply, and half of the disappearing females were found alive in the Hakone area. However, almost all female deserters disappeared again within three years. Moreover, fewer female deserters were found in the Hakone area in the scarce food supply period than in the abundant food supply period. Accordingly, when the food supply within the natal and adjacent ranges was scarce, not only natal males but also females may have dispersed to distant areas. In 1985, a new troop, consisting of about 20 monkeys, was discovered in an area located 7 km to the east of Mt. Myojingatake (Mr. T. IWANO, pers. comm.) which no Japanese monkey troops (except for solitary monkeys) had previously inhabited. There is a strong possibility that this troop was formed by female deserters of their offspring, because no troops in the Hakone area split into two after the P troop split into the P1 and P2 troops. The existence of the newly found troop supports the hypothesis mentioned above.

Many newcomers were attracted by the abundant food supply. However, the percentage of non-natal males to all resident males in the troop in the abundant food supply period was low, because the percentage of natal males which remained in the troop until 5 years of age during this period was higher than that in the scarce food supply period. A similar relationship, between the number of natal and non-natal males, can also be seen in the Arashiyama east troop. In the latter troop, the remaining rate of natal males of ages up to 5 years is about 70%, and about 20% of the natal males remain until the age of 10 years. Moreover, the number of non-natal males was only 2 for 7 years (KOYAMA, 1980; FEDIGAN et al., 1983). There is no adjacent troop in the vicinity of the Arashiyama troop, although some wild troops do live within 30 km of the troop. Judging from the fact that three tattooed natal T troop's males were found in the Hagachi troop, which is located about 60 km to the south of the T feeding site and which has been fed artificially since 1953, the small number of non-natal males in the Arashiyama troop must be based on the large number of natal males that remain. The large number of natal males must be based on an abundant artificial food supply, as was also estimated from the high birth rate (0.613), low infant mortality (0.104), and young primiparous age (5.6 years old) (KOYAMA, 1980). In fact, WOLFE (1984), who worked on the Arashiyama east troop, reported an abundant artificial food supply to the troop.

The amount of food resources including an artificial food supply in the home range may strongly influence the population parameters of Japanese monkeys. However, it has not yet been clarified how it influences the social organization or structure. Many researchers have pointed out that the pattern of food distribution can affect the foraging patterns or social organizations of primate species (WRANGHAM, 1977; KLEIN & KLEIN, 1977; WHEATLEY, 1980; VAN SHAIK & VAN NOORDWIJK, 1986; FUKUDA, in prep.). The amount of food, especially the artificial food supply, must exert an influence directly and/or indirectly on various social interactions among animals. Indeed, WOLFE (1984) argued that the abundant food supply minimized the competition among females.

Acknowledgements. Prof. Dr. Y. SUGIYAMA and Dr. K. WATANABE, Primate Research Institute, Kyoto University, kindly revised and commented on drafts of this manuscript. I would like to thank Mr. K. AKABORI, Dr. J. J. BURTON, Mr. M. MURAMATSU, Mr. K. SUZUKI, Mr. S. TANAKA, and other co-observers of Meisei University and Yokohama City University for their assistance, and Dr. T. ENOMOTO, Tokai University School of Medicine, for his help with the bibliography. I also wish to thank Mr. GENJI MIYAMOTO and other personnel of Yugawara Monkey Park for their kind help in the

observations, and Dr. S. KAWAMURA, Dr. M. KAWAI, Mr. S. AZUMA, Dr. A. SUZUKI, and other staff of the Primate Research Institute, Kyoto University, for their guidance and encouragement. Mr. D. S. SPRAGUE, Deptartment of Anthropology, Yale University, kindly revised the English of this paper. The present study was supported in part by the Cooperative Research Fund of the Primate Research Institute, Kyoto University, and the personal funds of my wife, YAEKO FUKUDA.

REFERENCES

BURTON, J. J. & F. FUKUDA, 1981. On female mobility: The case of the Yugawara-T group of *Macaca fuscata*. *J. Human Evol.*, 10: 381–386.

DITTUS, W. P. J., 1979. The evolution of behaviors regulation density and age-sex-distribution in the toque monkey. *Behaviour*, 69: 281–322.

DRICKAMER, L. C., 1974. A ten-year summary of reproductive data for free-ranging *Macaca mulatta*. *Folia Primatol.*, 21: 61–80.

FEDIGAN, L. M., H. GOUZOULES, & S. GOUZOULES, 1983. Population dynamics of Arashiyama west Japanese macaques. *Int. J. Primatol.*, 4: 307–321.

FUKUDA, F., 1982. Relationship between age and troop shifting in male Japanese monkeys. *Jap. J. Ecol.*, 32: 491–498. (in Japanese with English summary)

————, 1983. Troop desertion by female Japanese macaques. *Jap. J. Ecol.*, 33: 347–355. (in Japanese with English summary)

————, in prep. Habitual fission-fusion and social organization of a Japanese monkey troop at Hakone.

————, S. TANAKA, & M. MURAMATSU, 1974. Japanese monkeys in the Hakone mountains, I. *The Nihonzaru*, 1: 63–122. (in Japanese with English summary)

GOUZOULES, H., S. GOUZOULES, & L. FEDIGAN, 1982. Behavioral dominance and reproductive success in female Japanese monkeys (*Macaca fuscata*). *Anim. Behav.*, 30: 1138–1150.

KLEIN, L. L. & D. J. KLEIN, 1977. Feeding behaviour of the Colombian spider monkey. In: *Primate Ecology*, T. H. CLUTTON-BROCK (ed.), Academic Press, London, pp. 153–181.

KOFORD, C. B., 1965. Population dynamics of rhesus monkeys on Cayo Santiago. In: *Primate Behavior*, I. DEVORE (ed.), Holt, Rinehart, & Winston, New York, pp. 160–174.

KOYAMA, N., 1980. Demography of Japanese monkeys. In: *Research of Wild Animals in Japan* (*Nihon no Yasei wo Otte*), M. ASAHI (ed.), Tokai-daigaku-shuppan-kai, Tokyo, pp. 7–34. (in Japanese)

MATSUMOTO, F., 1985. *Standard Table of Food Composition* (*Shokuhin Seibun-Hyoh*). Shibata-shoten, Tokyo. (in Japanese)

MIYAKI, M., 1976. Is a stray dog a new wolf? (Atarashii Ookami ka). *Anima*, 45: 6–11. (in Japanese)

MOORE, J. & R. ALI, 1984. Are dispersal and inbreeding avoidance related? *Anim. Behav.*, 32: 94–112.

MORI, A., 1979. Analysis of population change by measurement of body weight in Koshima troop of Japanese monkeys. *Primates*, 20: 371–397.

NIEUWENHUIJSEN, K., A. J. J. C. LAMMERS, K. J. DE NEEF, & A. K. SLOB, 1985. Reproduction and social rank in female stumptail macaques (*Macaca arctoides*). *Int. J. Primatol.*, 6: 77–99.

SAMUELS, A., J. B. SILK, & P. S. RODMAN, 1984. Changes in the dominance rank and reproductive behaviour of male bonnet macaques (*Macaca radiata*). *Anim. Behav.*, 32: 994–1003.

SHAIK, C. P. VAN & M. P. VAN NOORDWIJK, 1986. The hidden costs of sociality: intra-group variation in feeding strategies in Sumatran long-tailed macaques (*Macaca fascicularis*). *Behaviour*, 99: 296–315.

SILK, J. B., C. B. CLARK-WHEATLEY, P. S. RODMAN, & S. SAMUELS, 1981. Differential reproductive success and facultative adjustment of sex ratios among female bonnet macaques (*Macaca radiata*). *Anim. Behav.*, 29: 1106–1120.

SIMPSON, M. J. A. & A. E. SIMPSON, 1982. Birth sex ratios and social rank in rhesus monkey mother. *Nature*, 300: 440–441.

SUGIYAMA, Y., 1976. Life history of male Japanese monkeys. In: *Advances in the Study of Behavior, Vol. 7*, J. S. ROSENBLATT, R. A. HINDE, E. SHAW, & C. BEER (eds.), Academic Press, New York, pp. 255–284.

———— & H. OHSAWA, 1982. Population dynamics of Japanese monkeys with special reference to the effect of artificial feeding. *Folia Primatol.*, 39: 228–263.

WHEATLEY, B. P., 1980. Feeding and ranging of East Bornean *Macaca fascicularis*. In: *The Macaques*, D. G. LINDBURG (ed.), Van Nostrand Co., New York, pp. 215–246.
WILSON, A. P. & R. C. BOELKINS, 1970. Evidence for seasonal variation in behavior by *Macaca mulatta*. *Anim. Behav.*, 18: 719–724.
WOLFE, L. D., 1984. Female rank and reproductive success among Arashiyama B Japanese macaques (*Macaca fuscata*). *Int. J. Primatol.*, 5: 133–143.
WRANGHAM, R. W., 1977. Feeding behaviour of chimpanzees in Gombe National Park, Tanzania. In: *Primate Ecology*, T. H. CLUTTON-BLOCK (ed.), Academic Press, London, pp. 503–538.

—Received *May 26, 1986*; Accepted *May 26, 1988*

Author's Name and Address: FUMIO FUKUDA, *2-27-12, Shohnandai, Fujisawa, Kanagawa, 252 Japan.*