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Reproduction of Wild Japanese Macaque Females of Yakushima and Kinkazan Islands: A Preliminary Report

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ABSTRACT. Wild Japanese macaque females of the Yakushima and Kinkazan populations exhibited similar reproductive features. (1) Births/female/year (BR: 0.27–0.35) was lower than those of provisioned troops, but (2) infant mortality (IM: 0.23–0.25) was higher than those of provisioned troops. (3) The interbirth interval (IBI) following the death of infants was 1.5–1.6 years, shorter than that following surviving infants (2.2–2.4 yrs). (4) Birth sex ratio (BSR) did not differ from 1:1. There was no consistent correlation between (5)female age and IM, (6) maternal rank and offspring BSR, or (7) maternal rank and reproductive success. On the other hand, (8) BR of Yakushima females was significantly lower than that of Kinkazan females. In particular, (9) Yakushima females stopped reproduction earlier than Kinkazan females, although (10) the first birth of Yakushima females was about one year earlier than Kinkazan females. (11) BR exhibited a humped curve against female age in Yakushima, but it was uncertain whether old-aged females of Kinkazan exhibited a post-reproductive life span (PRLS). (12) The survivorship for female juveniles was lower than that for male juveniles in Yakushima, whereas the survivorship for male juveniles was lower than that for female juveniles in Kinkazan. These data may indicate that Yakushima females more severely compete for resources than Kinkazan females, because of high population density, whereas the population density of Kinkazan might be limited by climate (e.g. heavy snow) rather than density dependent ecological effects.

Key Words: *Macaca fuscata fuscata*; *M. f. yakui*; Birth rate; Interbirth interval; Infant mortality; Survival curve.

INTRODUCTION

Recently, the reproductive parameters of female primates have aroused great interest among primatologists to assess the degree of female competition (FEDIGAN, 1983; HARCOURT, 1987). In particular, FEDIGAN et al. (1986) pointed out that the lifetime reproductive success of female primates should be analyzed to evaluate several modern interpretations of sexual selection theory, e.g. that female variance in reproductive success is insignificant in comparison to that of males, or that short-term evaluations of competitive success sufficiently reflect lifetime reproductive success.

Reproduction in Japanese macaque females has been analyzed in several provisioned troops (e.g. KOYAMA et al., 1992). However, there have been only a few reports about wild populations (e.g. SUZUKI et al., 1975), since it is difficult to carry out long term observations on wild

Japanese macaques. In this report, we present comparative data on several reproductive parameters of the wild populations of Yakushima and Kinkazan Islands, Japan. We preliminarily analyze their (1) birth rate (BR) and interbirth interval (IBI), (2) birth sex ratio (BSR), (3) infant mortality (IM), (4) survival curve, and (5) age-specific fecundity. We compare these data with those of provisioned populations or other non-provisioned populations in different habitats.

STUDY SITES AND METHODS

Data were collected from two populations of Japanese macaques, Yakushima Island (*Macaca fuscata yakui*) and Kinkazan Island (*M. f. fuscata*).

Yakushima Island is 70 km south of Kyushu Island in the Pacific Ocean (30°N, 130°E) with an area of 503 km^2. In the western coast, natural broadleaf evergreen forests extend from the coast to the mountainside of 800 m or over above sea level, where many macaque troops are continuously distributed. This area is not covered with snow even in winter. For further details on the vegetation and climate of the study site, see MARUHASHI (1982).

We analyzed the demographic data on females of the M-, T-, and P-troops. These troops branched from the Ko-troop between 1976 and 1977, and had been habituated from the 1970s without provisioning. From 1987, however, all of these three troops abruptly decreased in size. M-troop ceased to exist as an independent troop in 1989 (TAKAHATA et al., 1994), T-troop in 1993, and P-troop between 1992–1993 (SUGIURA et al., unpubl. data). In most cases, the remaining females joined the neighboring troops.

Kinkazan is a small island, with a total area of about 10 km^2, located 1 km east of Honshu Island in the Pacific Ocean (38°N, 141°E). This island is covered by the natural mixed forest of broadleaf deciduous and conifer trees, and is seldom covered with snow in winter. For further details on the vegetation and climate of the study site, see NAKAGAWA (1989).

Five troops have been observed without provisioning in Kinkazan Island (IZAWA, 1988, 1992, 1995, unpubl. data). In 1983, about 270 monkeys are estimated to have inhabited. However, in 1983 winter, many monkeys were dead because of heavy snow, and the population decreased to 180 in 1984. Then, the population gradually increased, and 200 monkeys are estimated to have inhabited in 1985, 222 in 1987, and about 260 in 1993. We analyzed the demographic data collected from 1983 to 1994 on the A-troop females, and those collected from 1983 to 1990 on the B2-troop females.

We compare such demographic data with those of two populations of Japanese macaques which have been intensively provisioned for about 30 years (Arashiyama troops: KOYAMA et al., 1992; Katsuyama troops: ITOIGAWA et al., 1992), and with those of two non-provisioned populations which inhabit snowy areas (Ryozen: SUGIYAMA & OHSAWA, 1982; Shiga Heights: SUZUKI et al., 1975). Statistical analysis were done on Lotus 1-2-3R5J (Lotus Development Co., Cambridge, 1994) and Statistica5J (StatSoft Inc., Tulsa, 1995).

RESULTS

BIRTHS, OFFSPRING SEX RATIO, AND INFANT MORTALITY

Yakushima

From 1974 to 1993, 76 infants were born to the females of M, T, and P troops (Table 1). Birth sex ratio (BSR) was 33:37, which did not significantly differ from 1:1 ($\chi^2=0.229$, $df=1$, $p>0.5$).

Table 1. Reproductive parameters of mature females aged 5 yr or more old in the Yakushima, Kinkazan, and other populations.

	Yakushima	Kinkazan	Ryozen	Shiga B2	Arashiyama	Katsuyama
Condition	Wild	Wild	Wild		Provisioned	Provisioned
Habitat	Evergreen forest	Deciduous/ conifer forest	Snowy deciduous/ conifer forest	Snowy deciduous/ conifer forest	Deciduous/ evergreen forest	Evergreen forest
(1)	282	275	134	63	1517	1828
(2)	76	97	45	22	816	905
(3)	0.270	0.353	0.336	0.349	0.538	0.495
(4)	33:37	56:40	–	–	410:390	428:477
(5)	0.25	0.227	0.277	0.533	0.103	0.102
(6)	Male>female	Male<female	–	–	–	–
(7)	6.1	7.05	–	–	5.39	5.41
(8)	1.5	1.59	–	–	1.15	1.29
(9)	2.24	2.37	–	–	1.46	1.58
Source	Present study	Present study	(10)	(11)	(12)	(13)

(1) Total of female-years; (2) total number of births; (3) births/female/year (BR); (4) birth sex ratio (BSR, males: females); (5) infant mortality within one year; (6) survivorship through the age of between 1 and 3 yr (see Figs. 1 & 4); (7) average age of females at first birth (yr); (8) average interbirth interval (IBI) following the death of infants within one year after birth (yr); (9) average IBI following surviving infants (yr); (10) SUGIYAMA & OHSAWA, 1982; (11) SUZUKI et al., 1975; (12) KOYAMA et al., 1992; TAKAHATA et al., 1995a; (13) ITOIGAWA et al., 1992.

Based on the pooled data recorded for the females aged 5 or more yr old, births/female/year (BR) was 0.270 (Table 1). This value was significantly lower than the BR of provisioned troops [0.538 in Arashiyama troops ($\chi^2=68.5$, $df=1$, $p=0.000$) and 0.495 in Katsuyama troops ($\chi^2=50.0$, $df=1$, $p=0.000$)], but did not significantly differ from BR reported for the non-provisioned troops [0.336 in Ryozen troop ($\chi^2=1.94$, $df=1$, $p=0.164$) and 0.349 in Shiga B2-troop ($\chi^2=1.61$, $df=1$, $p=0.205$)].

Infant mortality within one year after birth (IM) was 0.25, significantly higher than the 0.103 and 0.102 reported for the provisioned Arashiyama and Katsuyama troops ($\chi^2=15.13$ and 15.31, $df=1$, $p=0.0001$) (Table 1). On the other hand, this value did not significantly differ from IM reported for the Ryozen troop (0.277) ($\chi^2=0.11$, $df=1$, $p=0.744$). Meanwhile, it was lower than from 0.533 reported for Shiga B2-troop which inhabited the snowy Shiga Heights. This difference was nearly significant (two-tailed Fisher's exact probability test, $p=0.059$).

Kinkazan

From 1983 to 1994, 97 infants were born to the females of A- and B2-troops (Table 1). BSR was 56:40, which did not significantly differ from 1:1 ($\chi^2=2.67$, $df=1$, $p>0.1$). Pooled data for the females aged 5 or more yr old indicated that the BR of 0.353 was significantly higher than that of the Yakushima troops ($\chi^2=4.50$, $df=1$, $p=0.0338<0.05$). On the other hand, this value was significantly lower than those of Arashiyama and Katsuyama troops ($\chi^2=31.9$ and 19.4, $df=1$, $p=0.000$ and 0.000), but it did not differ from those reported for the Ryozen and Shiga B2-troops ($\chi^2=0.11$ and 0.00, $df=1$, $p=0.736$ and 0.958).

The IM of 0.227 did not significantly differ from that of Yakushima troops ($\chi^2=0.13$, $df=1$, $p=0.722$) (Table 1). This value was significantly higher than those of Arashiyama and Katsuyama troops ($\chi^2=13.37$ and 13.55, $p=0.0003$ and 0.0002), but it did not significantly differ from IM reported for the Ryozen troop (0.277) ($\chi^2=0.43$, $df=1$, $p=0.513$). Meanwhile, it was significantly lower than IM of Shiga B2-troop (two-tailed Fisher's exact probability test, $p=0.0243$).

SURVIVAL CURVE AND AGE-SPECIFIC FECUNDITY

Yakushima

In M-, T-, and P-troops, 36 females were born and died from 1974 to 1993. For these females, a survival curve was drawn (Fig. 1). For the 26 males born into the same population, a curve showing survival/remaining within the natal troop was also drawn (Fig. 1).

Average female life span was 6.3 yr (n=36, sd=5.2 yr). Through the age of between 1 and 3 yr, female survivorship tended to be lower than that of males, but these differences were not significant [two-tailed Fisher's exact probability test, p=0.529 (at the age of 1 yr), p=0.553 (2 yr), and p=0.781 (3 yr)].

The average age of females at first birth was 6.1 yr (n=17, sd=0.9) (Fig. 2a). For first infants, IM was 0.353, which was higher than that for the second or later infants (0.220), but the difference was not significant (χ^2=1.24, p=0.266). Mean interbirth interval (IBI) following the death of infants within one year after birth was 1.5 yr (n=6, sd=0.84), significantly shorter than that following surviving infants (m=2.24 yr, n=42, sd=0.85) (Mann Whitney U-test, z=2.02, p=0.043<0.05). On the other hand, there was no significant difference between IBI following surviving male infants (m=2.17 yr, n=23, sd=0.78) and that following surviving female infants (m=2.32, n=19, sd=1.0) (z=0.331, p=0.741).

BR exhibited a humped curve against female age (Fig. 3). BR was low for the 5-yr-old females, and it ranged from 30 to 40% for the females between 6 and 13 yr of age. Then, BR abruptly decreased for the females aged 15 or more yr old. Thus, most old-aged females experienced a post-reproductive life span (PRLS) before their deaths. On the other hand, there is no consistent correlation between IM and female age.

The 31 females who survived to the age of 5 yr produced 2.26 offsprings on average (sd=2.1, range 0–9) during their remaining life span. Of these offspring, 0.71 female infants survived to the age of 5 yr (sd=1.1, range 0–4).

Males began to leave their natal troops from the age of 3 yr (see Fig. 1). Of the 19 males who survived to the age of 3 yr, 17 males disappeared from their natal troops by the age of 7 yr. Out of them, at least six males were observed to transfer into the neighboring troops at the age of 4.5 yr on average (sd=1.05, range 3–6 yr).

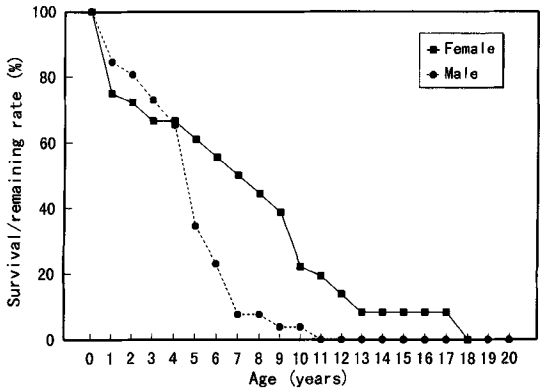

Fig. 1. Survive/remaining within the natal troop curves for the monkeys born into Yakushima population from 1974 to 1993.

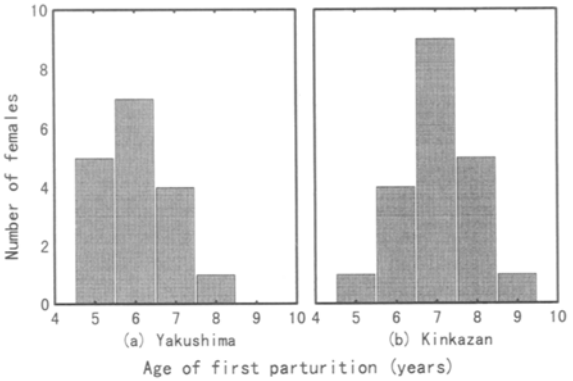

Fig. 2. Female's age at the first parturition in (a) Yakushima and (b) Kinkazan populations.

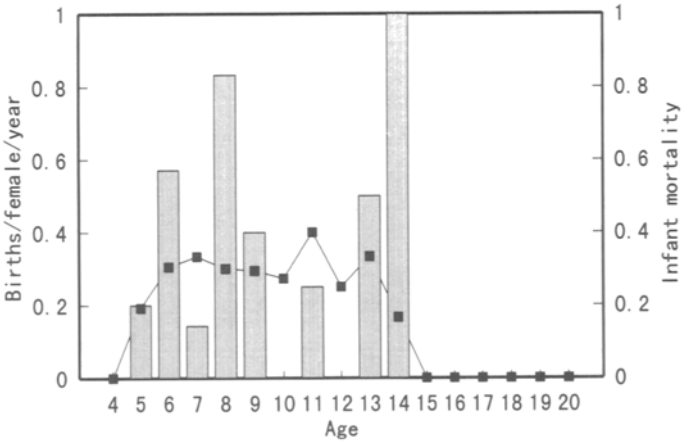

Fig. 3. Female age, BR (line graph), and IM (bar graph) of Yakushima population.

Kinkazan

For the 31 males and 18 females born to Kinkazan A- and B2-troops from 1980 to 1989, age-curves for survival and/or remaining within the natal troop were calculated up to the age of 5 yr (Fig. 4). There is a consistent tendency for female survivorship to be higher than that of males. This difference is significant at the age of 1 yr (two-tailed Fisher's exact probability test, $p=0.0379<0.05$), but not significant at the ages of 2–3 ($p=0.095$ and 0.095). Out of 18 female infants, 15 females (83%) survived to the age of 5 yr. This rate was higher than that of Yakushima (61%), although the difference was not significant (two-tailed Fisher's exact probability test, $p=0.127$).

The average age of at first birth was 7.05 yr ($n=20$, $sd=0.94$), significantly later than the females of Yakushima (Mann Whitney U-test, $z=2.92$, $p<0.01$) (see Fig. 2b). For first infants, IM was 0.350, not significantly different from that of second or later infants (0.195) ($\chi^2=2.18$, $df=1$, $p=0.1398$).

Mean IBI following the death of infants within one year after birth was 1.59 yr ($n=17$,

sd=0.62) (Table 1). This value was almost equal to that of Yakushima, being significantly shorter than that following surviving infants (n=49, m=2.37 yr, sd=0.57) (Mann Whitney U-test, z=4.05, p<0.0001). There was no significant difference between mean IBI following surviving male infants (n=27, m=2.41 yr, sd=0.64) and that following surviving female infants (n=22, m=2.32 yr, sd=0.48) (z=0.530, p=0.596). There was also no significant difference in IBI following surviving infants between the Kinkazan and Yakushima populations (z=1.11, p=0.267).

BR was low for the 5- and 6-yr-old females, and it ranged from 40 to 50% for the females between 6 and 19 yr of age (Fig. 5). In contrast to the females of Yakushima, BR scarcely decreased for the females aged 20 or more yr old; the old-aged females of Kinkazan may have maintained higher fecundity than females of Yakushima.

There was no consistent correlation between the IM and female age (Fig. 5). IM tended to be high for the 6−8-yr-old females and 13−18-yr-old females. On the other hand, it was low for the females aged 9 to 12 yr old and >19 yr old.

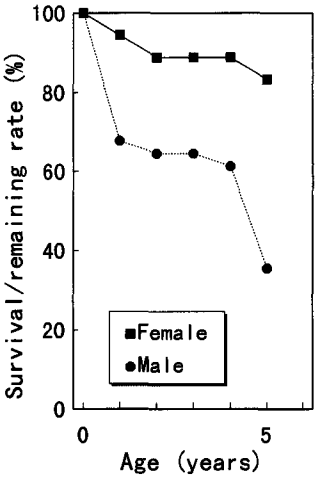

Fig. 4. Survive/remaining within the natal troop curves for the monkeys born into Kinkazan population from 1980 to 1989.

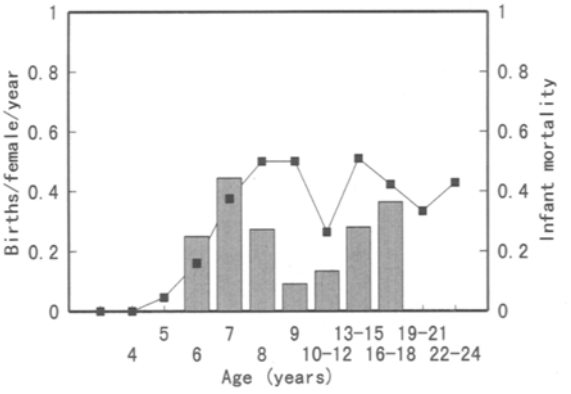

Fig. 5. Female age, BR (line graph), and IM (bar graph) of Kinkazan population.

Males began to leave their natal troops from the age of 3 yr (Fig. 4). Of the 21 males who survived to the age of 3 yr, 16 males disappeared from their natal troops by the age of 6 yr.

Reproductive Success and Dominance Rank of Females

Yakushima

In M-group, long-lasting and stable dominance relations among female kin-groups have been observed (Hill & Okayasu, 1995). However, there was no consistent correlation between female rank-groups and their lifetime reproductive success (Fig. 6). First, no significant difference existed in BR among female rank-groups (Kruskal-Wallis test, $H=2.621$, $df=2$, $p=0.270$) (Fig. 6a), number of lifetime offspring ($H=0.067$, $df=2$, $p=0.967$) (Fig. 6b), or number of daughters who survived to the age of 5 yr ($H=0.321$, $df=2$, $p=0.852$) (Fig. 6c). There was also no significant difference in IM among them ($H=3.42$, $df=2$, $p=0.181$) (Fig. 6d).

There was no significant difference in BSR among female rank-groups ($\chi^2=1.065$, $df=2$, $p>0.5$). Similarly, there was no significant difference in the age of first birth among them ($H=3.495$, $df=2$, $p>0.1$).

Kinkazan

There was no significant difference in BR among three female rank-groups (A-troop: $\chi^2=0.198$, $df=2$, $p>0.9$; B2-troop: $\chi^2=0.938$, $df=2$, $p>0.6$) (Table 2). There was also no significant difference in the age at first birth among female rank-groups (A-troop: Kruskal-Wallis test, $H=0.935$, $df=2$, $p>0.6$; B2-troop: $H=0.883$, $df=2$, $p>0.6$).

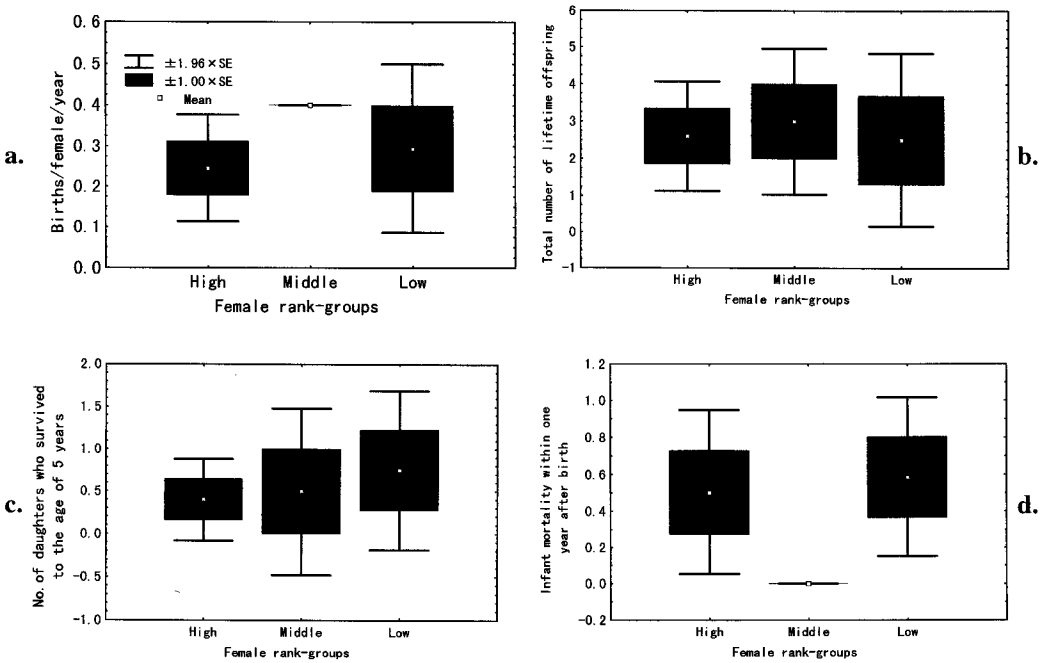

Fig. 6. Female rank-groups and **a.** BR, **b.** number of lifetime offspring, **c.** number of daughters who survived to the age of 5 yr old, and **d.** IM in Yakushima M-troop.

Table 2. Female rank and reproductive parameters of Kinkazan population.

	Mother's rank					
	A-troop			B2-troop		
	High	Middle	Low	High	Middle	Low
Total of female-years	60	61	56	41	28	29
Total number of births	26	25	22	11	5	8
BR	0.433	0.410	0.393	0.268	0.179	0.276
Age at first birth (yr)	6.6	7.2	6.7	7.0	7.7	8.0
BSR (males: females)	14:12	15:10	15:7	7:4	3:2	2:5
IM	0.231	0.24	0.409	0.091	0.00	0.00

There was no significant difference in BSR ($\chi^2=1.024$, $df=2$, $p>0.5$) nor IM ($\chi^2=2.271$, $df=2$, $p>0.3$) among three female rank-groups of A-troop (Table 2). In B2-troop, low-ranking females tended to give birth to more female infants than male infants, but these differences were not significant ($\chi^2=2.265$, $df=2$, $p>0.3$). There was also no significant difference in IM among female kin-groups ($\chi^2=1.233$, $df=2$, $p>0.5$).

DISCUSSION

General Features of the Reproductive Parameters of Wild Japanese Macaque Females

On the whole, wild Japanese macaque females of the Yakushima and Kinkazan populations exhibited similar reproductive features to other non-provisioned populations, but they differed from those of provisioned populations, as follows (see Table 1).

First, BR was 0.27−0.35, significantly lower than those of the provisioned populations such as Arashiyama and Katsuyama troops, but was not different from those reported for the non-provisioned populations such as Ryozen or Shiga B2-troops (Table 1). In the census carried out in 1990−1993 on the wild troops inhabiting the coast area of Yakushima Island, the ratio of infants to the mature females within a troop was 0.326 ($sd=0.286$), being similar to the present data (Yoshihiro et al., unpubl. data).

Second, IM was higher than those of provisioned troops. The present value (0.23−0.25) was significantly higher than those (about 0.10) of Arashiyama and Katsuyama troops, but was not different from that reported for the non-provisioned Ryozen population (Table 1). However, it was much lower than that of the Shiga B2-troop inhabiting a snowy, mountainous area. One of the causes of high IM of Shiga B2-troop might be the heavy snow fall in winter (Suzuki et al., 1975).

Third, IBI following the death of newborn infants was 1.5−1.6 yr, shorter than IBI following successful rearing the infants (2.2−2.4 yr) (Table 1). On the other hand, infant sex had no effect on subsequent interbirth intervals. For the mothers of wild Japanese macaques, there may be no significant difference in the cost to produce between sons and daughters, differing from the data reported for captive long-tailed macaques (*Macaca fascicularis*) (van Schaik et al., 1989) and Arashiyama troops (Takahata et al., 1995a), which suggest that female infants are more costly to produce than male infants.

Fourth, BR was low for 5-yr-old females, and it increased and ranged from 30 to 40% for the middle-aged females. On the other hand, there was no consistent correlation between the IM and female age.

Do High-ranking Females Attain High Reproductive Success?

It often has been proposed that high-ranking primate females attain high reproductive success, but the data are contradictory [see Fedigan (1983) and Harcourt (1987) for review]. Some reports indicated a clear correlation between female rank and reproductive success (*Macaca mulatta*: Drickamer, 1974; *Papio cynocephalus*: Smuts & Nicolson, 1989), but others failed to find such a relation (e.g. *Cercopithecus aethiops*: Cheney et al., 1988).

The present data showed that there was no consistent correlation between female rank and reproductive success, just as reported for the Arashiyama East and West populations of Japanese macaques (Wolfe, 1984; Fedigan et al., 1986; Koyama et al., 1992). Of course, this does not mean that females actually do not compete with one another in a wild/non-provisioned environment (see, Hill & Okayasu, 1995). Troop fissions frequently occurred in the Yakushima population (Maruhashi, 1982), which may suggest the existence of severe intra-troop competition. However, such female competition might not be directly reflected in rank related individual reproductive success within a troop.

It has been proposed that the primate females vary offspring sex ratio according to the sociological and/or ecological conditions (van Schaik & Hrdy, 1991). In the present study, however, BSR was not significantly different from 1:1, and there was no consistent difference in BSR among female kin-groups. Thus, just as reported for the provisioned population of Japanese macaques (Koyama et al., 1992; Itoigawa et al., 1992), the present data support neither the Trivers-Willard (1973) model, which predicts that high-rank mothers should produce more sons (male quality hypothesis), nor the Silk (1983) model, which predicts that high-rank mothers should produce more daughters (advantaged daughter hypothesis).

Discrepancies Between Yakushima and Kinkazan Populations

There were several discrepancies in female reproductive parameters between Yakushima and Kinkazan populations (Table 1).

First, BR of the Yakushima population was significantly lower than that of the Kinkazan population. This may partly result from the abrupt decrease in size and reproduction by the M-, T-, and P-troops in the period of 1987−1993. In the Yakushima population, there is a tendency that the BR of troops with small size (<about 14 individuals) is lower than that of the larger troops (Takahata et al., unpubl. data).

Second, the Yakushima females stopped reproducing quite earlier than the Kinkazan females (see Figs. 3 & 5), although the latter began to give birth about one year earlier than the formers (Table 1). Thus, some old Yakushima females showed a clear PRLS before their death (Takahata et al., 1995b), and BR exhibited a humped curve against female age, as reported for the provisioned troops (e.g. Koyama et al., 1992). In contrast, it was uncertain whether the old females of Kinkazan exhibited such a PRLS.

Third, it has been proposed that there may be a sexual difference in juvenile mortality within a primate population (van Schaik & Visser, 1990). In Yakushima, the survivorship for female juveniles was lower than that for male infants (Fig. 1), which may correspond to "harassed daughter" hypothesis proposed by van Schaik and Visser (1990). In contrast, the survivorship for male juveniles was lower than that for female juveniles in Kinkazan (Fig. 4).

These data may mean that the Kinkazan females attain higher lifetime reproductive success than the Yakushima females. Of course, there is a possibility that these discrepancies may be due to the genetic differences between these two subspecies (i.e. *Macaca fuscata fuscata* vs *M.*

f. yakui). However, these discrepancies may originate in the severe female competition for resources in Yakushima, probably because of high population density. In the study area of Yakushima, population density may have increased from 33 monkeys/km^2 (estimated in the 1970s by MARUHASHI, 1982) to 38.6–81.5 monkeys/km^2 (estimated in 1990, calculated from the census data by YOSHIHIRO et al., unpubl.), although the cause is uncertain. Such a high population density may have caused severe competition over food resources and social stress, which might be reflected in the low BR or survivorship of Yakushima females. Whereas, the population density of Kinkazan is estimated to have ranged from 18 to 28 monkeys/km^2 during the study period (calculated from the demographic data by IZAWA, 1992, 1995, unpubl. data). In Kinkazan, the population density of monkeys might be limited by climate (e.g. heavy snow) rather than density dependent ecological effects (IZAWA, 1988).

However, there are inadequate data to confirm these hypotheses. Further long-term field study should be expected in these two populations of wild Japanese macaques.

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REFERENCES

CHENEY, D. L.; SEYFARTH, R. M.; ANDELMAN, S. J.; LEE, P. C. 1988. Reproductive success in vervet monkeys. In: *Reproductive Success*, CLUTTON-BROCK, T. H. (ed.), Univ. of Chicago Press, Chicago, pp. 384–402.

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

FEDIGAN, L. M. 1983. Dominance and reproductive success in primates. *Ybk. Phys. Anthropol.*, 26: 91–129.

FEDIGAN, L. M.; FEDIGAN, L.; GOUZOULES, S.; GOUZOULES, H.; KOYAMA, N. 1986. Lifetime reproductive success in female Japanese macaques. *Folia Primatol.*, 47: 143–157.

HARCOURT, A. H. 1987. Dominance and fertility among female primates. *J. Zool. Lond.*, 213: 471–487.

HILL, D. A.; OKAYASU, N. 1995. Absence of 'youngest ascendency' in the dominance relations of sisters in wild Japanese macaques (*Macaca fuscata yakui*). *Behaviour*, 132: 367–379.

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.

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

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. Edu.*, 27: 69–75. (in Japanese with English Summary)

IZAWA, K. 1995. The ecological study of wild Japanese monkeys living in Kinkazan Island, Miyagi Prefecture: on the population change in recent three years. *Bull. Miyagi Univ. Edu.*, 30: 147–157. (in Japanese with English Summary)

KOYAMA, N.; TAKAHATA, Y.; HUFFMAN, M. A.; NORIKOSHI, K.; SUZUKI, H. 1992. Reproductive parameters of female Japanese macaques: thirty years data from the Arashiyama troops, Japan. *Primates*, 33: 33–47.

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

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

VAN SCHAIK, C. P.; HRDY, S. B. 1991. Intensity of local resource competition shapes the relationship between maternal rank and sex ratios at birth in cercopithecine primates. *Amer. Naturalist*, 138: 1555–1562.

VAN SCHAIK, C. P.; NETTO, W. J.; VAN AMERONGEN, A. J. J.; WESTLAND, H. 1989. Social rank and sex ratio of captive long-tailed macaque females (*Macaca fascicularis*). *Amer. J. Primatol.*, 19: 147–161.

VAN SCHAIK, C. P.; DE VISSER, J. A. G. M. 1990. Fragile sons or harassed daughters?: sex differences in mortality among juvenile primates. *Folia Primatol.*, 55: 10–23.

SILK, J. A. 1983. Local resource competition and facultative adjustment of sex ratios in relation to competitive abilities. *Amer. Naturalist*, 121: 56–66.

SMUTS, B. B.; NICOLSON, N. 1989. Reproduction in wild female olive baboons. *Amer. J. Primatol.*, 19: 229–246.

SUGIYAMA, Y.; OHSAWA, H. 1982. Population dynamics of Japanese monkeys with special reference to the effect of artificial feeding. *Folia Primatol.*, 39: 238–263.

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. *Phys. Ecol.*, 16: 15–23. (in Japanese)

TAKAHATA, Y.; KOYAMA, N.; HUFFMAN, M. A.; NORIKOSHI, K.; SUZUKI, H. 1995a. Are daughters more costly to produce for Japanese macaque mothers?: sex of the offspring and subsequent interbirth intervals. *Primates*, 36: 571–574.

TAKAHATA, Y.; KOYAMA, N.; SUZUKI, S. 1995b. Do the old aged females experience a long post-reproductive life span?: the cases of Japanese macaques and chimpanzees. *Primates*, 36: 169–180.

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

TRIVERS, R. L.; WILLARD, D. E. 1973. Natural selection of parental ability to vary the sex ratio of offspring. *Science*, 179: 90–92.

WOLFE, L. D. 1984. Female rank and reproductive success among Arashiyama B Japanese macaques (*Macaca fuscata*). *Int. J. Primatol.*, 5: 133–143.

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