Maternal investment in sons and daughters in provisioned, free-ranging Japanese macaques (*Macaca fuscata*)

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Abstract It has been suggested that the physical condition of a mother may affect her pattern of investment in her sons or daughters. In addition, when competition over local resources becomes intense, severe aggression among the philopatric sex leads to a higher mortality of the sex and a biased birth sex ratio toward the opposite sex in the low rank. Parental sex-biased investment has been studied in many animal species to test these hypotheses, but the results have been highly inconsistent. We examined maternal sex-biased investment in relation to dominance rank using data on infant growth, infant mortality, birth sex ratio, and delay of subsequent reproduction by rearing current offspring from a provisioned, free-ranging Japanese macaque (*Macaca fuscata*) troop at Takasakiyama, Japan. The results showed that there was no sex difference in infant body mass among offspring of high- and low-ranking females. Use of the logistic regression model to analyze infant mortality with several independent variables failed to show a statistically significant sex bias. Birth sex ratio did not differ significantly between high- and low-ranking females. Among high-ranking females, there was no significant difference in delivery rate in the next year between those that reared a son and those that reared a daughter. For low-ranking females, however, the delivery rate after rearing daughters was markedly lower than that after rearing sons. Thus, there was no evidence of statistically significant maternal male-biased investment. For low-ranking females, we found a delay in subsequent reproduction for mothers after rearing daughters and no sex difference in offspring mortality. These results suggest that the females increased their offspring’s chances of survival, irrespective of sex, by postponing their subsequent delivery.

Key words: sex difference, maternal investment, dominance rank, *Macaca fuscata*

Introduction

Parental investment in sons and daughters has been studied in many animal species (reviewed by Clutton-Brock, 1991; Brown, 2001). Trivers and Willard (1973) suggested that maternal physical condition, i.e. nutritional status and health condition, affects the pattern of investment in sons or daughters. For polygynous species, this hypothesis leads to the prediction that mothers in good condition should invest more in sons than in daughters, while those in poor condition should invest more in daughters than in sons. This prediction is based on the assumption that body size in adulthood influences the reproductive success of males more than that of females because only winners of conflicts among males can mate with females and variability in individual fitness is greater among males than females in harem-forming mammals. The prediction was proved in red deer, *Cervus elaphus* (Clutton-Brock et al., 1984, 1986).

Although various results on skewed sex ratio at birth have been reported in many animal species (Clutton-Brock, 1991), the birth sex ratio in humans is 51:49 (males : females) throughout the world (Hrdy, 1999). After birth, however, human parents often bias investment, including food, protection, education, and inheritance of property, toward either sons or daughters during a long rearing period (Hrdy, 1999). For example, female infanticide is common in the highest class of a north Indian tribe (Dickmann, 1979). The causes of female infanticide in this class are (i) the difficulty for women to find a husband according to a rule that a woman should marry a man belonging to a higher class than herself; and (ii) the difficulty for parents to give an enormous dowry upon their daughter’s marriage. The quality and quantity of parental investment toward a child are affected by whether the sex of the child and the sibling composition meet the desirable standards of the community and/or class of parents (Hrdy, 1999); however, there are few comparative studies on the relationships between sex-biased parental investment and community standards. These comparative studies need information, such as the birth sex ratio, infanticide, child mortality, the number of children per family, property, and the hierarchy and marriage system in the community.
Investigators do not have access to the actual state of delivery, parental care, and filicide in humans; hence, the collected data may not reflect the facts (Daly and Wilson, 1988). Results of research based on direct observation in nonhuman primates, which, like humans, have long lifespans and complex societies, may contribute considerably to our understanding of parental investment in humans.

Among the many studies on sex-biased investment in nonhuman primates that have been conducted, some support the Trivers and Willard (1973) prediction (e.g. Paul and Kuester, 1990); some indicate an opposite trend (e.g. Simpson and Simpson, 1982); and some suggest similar investments in both sexes (e.g. Koyama et al., 1992). Thus, previous studies are highly inconsistent (Brown, 2001). A cause of such inconsistency is the variation in the intensity of local resource competition (LRC) among populations. LRC is defined as competition among animals of the philopatric sex over local resources (Clark, 1978). When this competition becomes intense, severe aggression among the philopatric sex leads to a higher mortality and a biased birth sex ratio toward the opposite sex in the low rank. Trivers and Willard’s prediction can be expressed only when the competition for local resources is relaxed (van Schaik and Hrdy, 1991). Thus, the intensity of LRC affects the birth sex ratio and the sex difference in infant and/or juvenile mortality in primates.

To examine how parents divide investment between sons and daughters, information is needed on offspring mortality and growth, the delay of subsequent reproduction for the parents of rearing offspring, and birth sex ratios. However, no such information is available for any population of primates (Brown, 2001). Although it is not easy to quantitatively evaluate the physical condition of the mother and the intensity of LRC, such factors can be evaluated indirectly. Dominance rank may be an appropriate index of physical condition (Brown, 2001; Brown and Silk, 2002), and when LRC is intense in female-philopatric species, daughters of low-ranking females should be more likely to die compared with other infants, and the proportion of males born to low-ranking females should be greater than the proportion born to high-ranking females (Silk, 1983).

Although provisioning improved reproductive parameters and led to an increase in the difference between dominance ranks in reproductive parameter values (Sugiyama and Ohsawa, 1982; Kurita et al., 2008), there is the advantage that provisioned populations have accumulated abundant data on reproduction because of long-term research and large population sizes. Provisioned Japanese macaques (Macaca fuscata) are useful to examine sex-biased maternal investment using various parameters based on large sample size because inconsistent, but interesting, results have been reported—a male-biased birth sex ratio among high-ranking females (Aureli et al., 1990), longer interbirth intervals after rearing daughters than after sons (Takahata et al., 1995), and no sex-biased maternal investment (Koyama et al., 1992). There are abundant data on reproduction and infant growth in a provisioned, free-ranging Japanese macaque population at Takasakiyama, in the southern region of Japan (Kurita et al., 2002, 2008). In this study, we examine infant mortality, birth sex ratio, delay of subsequent reproduction as the cost to the mother, and infant body mass in relation to maternal dominance rank and infant sex for Troop C of Japanese macaques at Takasakiyama. Birth sex ratio reflects maternal investment toward fetuses, although details of the mechanism are unknown. In contrast, sex difference in infant mortality reflects not only maternal investment from the fetus until infant stage but also the threats faced by the infant, e.g. attack from group members or predators.

**Methods**

**Study troop**

We conducted this study on Troop C, for which more data on reproduction and body mass are available than for Troops A and B, at Takasakiyama Natural Zoo, Oita Prefecture, southern Japan. The birth season at Takasakiyama extends from April to September (Kurita et al., 2008). The ranges of troop size and number of females aged 5 years or older in Troop C between 1987 and 2009 were 422–836 and 137–365, respectively (Oita City, 1987–2009). We used data for the seven years between 1987 and 1993 to analyze infant mortality, sex ratio at birth, and delay of subsequent reproduction, and used data for the nine years of 1997 and 2002–2009 to analyze infant body mass (see below and Table 1). Provisioning affects the nutritional levels and reproductive performance of animals (e.g. Sugiyama and Ohsawa, 1982). However, because the amount of provisioned food per animal and the ways of feeding these macaques have not been changed since 1981 at Takasakiyama (Kurita et al., 2008), we concluded that we could deal equally with the two periods from the viewpoint of amount of provisioned foods, food distribution pattern, and, as a result, intensity of LRC, for Troop C animals.

**Body mass measurement**

The infants, excluding offspring of primiparous females, born in 1997 and between 2002 and 2009, and their mothers, were weighed by one of the authors (H.K.) between July 1997 and August 1998 and between April 2002 and March 2010 on a longitudinal basis using a 20 kg capacity spring dial scale (Yamato SD-20). The masses of adult females, adult females holding infants, and infants were recorded to the nearest 0.05 kg. Where it was possible to measure both the mass of an adult female holding her infant and that of the adult female alone within 30 min, the infant’s mass was obtained by subtracting the adult female’s mass from their combined total. Because peanuts were used as an incentive to lure animals to the scale, infants of low- and middle-

**Table 1. Parameters examined**

<table>
<thead>
<tr>
<th>Parameter</th>
<th>When data were collected</th>
<th>Sample size (H, M, L)*</th>
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</thead>
<tbody>
<tr>
<td>Infant body mass</td>
<td>1997 and 2002–2009</td>
<td>(58, 18, 14)</td>
</tr>
<tr>
<td>Infant mortality</td>
<td>1987–1993</td>
<td>(112, 64, 92)</td>
</tr>
<tr>
<td>Sex ratio at birth</td>
<td>1987–1993</td>
<td>(133, 98, 112)</td>
</tr>
<tr>
<td>Delivery rate the follow-</td>
<td>1987–1993</td>
<td>(19, 16, 19)</td>
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<td>ing year</td>
<td></td>
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* H, M, and L mean sample sizes of the three dominance ranks of mothers: H, high ranking; M, middle ranking; L, low ranking.
Maternal investment: infant body mass at 180 days of age

We compared infant body mass at 6 months of age (180 days), as a proxy of maternal investment, between the sexes among offspring of high- and low-ranking females. According to Tanaka (1992), the daily rate of milk transfer from mother to infant in Japanese macaques is stable from birth up to 5 months of age and declines abruptly at 6 months. A study of one free-ranging Japanese macaque infant showed that it began to feed intensively on its own from 5 or 6 months of age and defined body mass at 6 months of age as the rough outcome of maternal investment through milk.

For individuals that were measured one or more times, both between 120 and 179 days and between 180 and 240 days, we estimated mass at 180 days of age. Because the body mass of Takasakiyama macaques increases linearly from birth to 300 days of age (Kurita et al., 2002), we generated a linear regression line using data between 120 and 240 days, inclusive, with Excel, and estimated mass at 180 days to the nearest 0.05 kg.

Data on birth and survival

Data on birth and survival for the seven years between 1987 and 1993 were analyzed. Birthdates and infant sex were recorded by one of the authors (T.M.) and other zoo staff members. T.M. checked the survival of each infant once per month from birth to the end of the following May for each cohort born between 1987 and 1993, and regarded infants that had disappeared within the survey as having died.

We only used data on births and infant deaths for females whose dominance rank, maternal age, offspring sex, and birthdates were known and also whose maternal age was between 8 and 19 years old to examine relationships between physical condition and reproductive output. Although Kurita (2010) found no dataset showing a significant difference in an investigation of sex differences in infant mortality rates in five provisioned Japanese macaque populations, infant sex was the only variable considered in that study. In the present study, therefore, we used the logistic regression model, which can evaluate an effect of each independent variable on a dependent variable excluding effects of other variables (Sokal and Rohlf, 1995), to examine effects of such factors as sex, maternal dominance rank, maternal reproduction in the previous year, birth year, and birth month on mortality. We chose to study infants during their first year of life rather than juveniles for two reasons. First, we were interested in the maternal investment for rearing dependent offspring; second, it is often difficult to discriminate between juvenile male deaths and emigration from the natal troop. Some studies demonstrated a sex difference in mortality among the immature offspring of low-ranking females but not among those of high-ranking females (e.g., Silk, 1983). We therefore added the interaction between infant sex and maternal dominance rank to the above variables.

In the analysis of sex ratio at birth, data from 1987 to 1993 were used.

Delay of subsequent reproduction

While we analyzed infant mortality for loss of current offspring, we examined delivery rate in the next year as an index of delay of subsequent reproduction caused by deterioration of maternal nutritional state because of investment in current offspring. We examined whether females who reared offspring born in a given year, referred to as ‘Year 1,’ until at least the end of the following May in the next year, referred to as ‘Year 2,’ could give birth to another offspring in that following year (Year 2) by using data from 1987 to 1993. The two years subsequent to Year 2 were referred to as ‘Year 3’ and ‘Year 4.’

We checked delivery records to determine whether a particular female was living in Troop C in any given year as a matter of convenience because the size of this troop is so large (see above). Because most interbirth intervals for Takasakiyama females were between 1 and 3 years (Soumah and Yokota, 1992), for females whose name we could find in the delivery records at least once between Years 2 and 4, we examined whether they had given birth again in Year 2. To eliminate any effect of reproduction in the previous year (Year 0) on maternal nutritional condition, we eliminated females whose names we found on delivery records in Year 0. Regarding Year 1, we excluded females under 8 and over 19 years from the data.

Maternal dominance rank

For data between 1987 and 1993, one of the authors (T.M.) divided mothers aged 6 years or more into high-, middle-, and low-ranking groups mainly on the basis of the records of outcome between two individuals in peanut tests. In the data for 1997 and 2002–2009, another author, H.K., also divided mothers of focal infants into three ranks. To clearly examine the differences related to maternal dominance rank, analyses were restricted to data from high- and low-ranking mothers, although data from middle-ranking females were also shown.

Statistical procedures

The logistic regression was calculated with the SAS CATMOD, categorical data modeling, Procedure (SAS Institute Inc., 1988) to examine effects of such factors as sex, maternal dominance rank, maternal reproduction in the previous year, birth year, and birth month on mortality. Fitness of a generated model was evaluated with likelihood ratio. When a probability calculated by a test of goodness of fit with likelihood ratio is larger than 0.05, the generated model is not significantly different from a model with a perfect fit, i.e. it can be considered that a fitted model is generated. We used the Mann–Whitney U-test for comparisons of infant body mass and Fisher’s exact test for analyses of sex ratio at birth and in delivery rates, with SPSS 11.0 J (SPSS Inc., 1995, 2001). When we made independent significance tests k times, we set the significance value at 0.05/k using the Bonferroni method (Sokal and Rohlf, 1995). For three independent tests, among males vs. females of high and low ranks
and among the offspring of high- vs. low-ranking females on infant body mass, we set the significance value at 0.016. For two tests on delivery rate in the subsequent year among the high- and low-ranking females, we set the value at 0.025.

Results

Infant body mass
Mean body masses at 180 days of age for both sexes of the three dominance ranks were as follows:

- **High ranking**:
  - males: \( n = 26 \), mean = 1413 g;
  - females: \( n = 32 \), mean = 1400 g;

- **Middle ranking**:  
  - males: \( n = 12 \), mean = 1313 g;
  - females: \( n = 6 \), mean = 1375 g;

- **Low ranking**:  
  - males: \( n = 8 \), mean = 1125 g;
  - females: \( n = 6 \), mean = 1125 g.

There was no significant sex difference among offspring of high- or low-ranking females (high: Mann–Whitney \( U \)-test, \( U_{\text{cal}} = 395.5 \), \( z = -0.323 \), \( P = 0.752 \), two-tailed; low: \( U_{\text{cal}} = 23 \), \( z = -0.131 \), \( P = 0.930 \), two-tailed; Figure 1). When data from both sexes were pooled because of the lack of significant sex differences, offspring of high-ranking mothers were significantly heavier than those of low-ranking mothers (high: \( n = 58 \), mean = 1406 g; low: \( n = 14 \), mean = 1125 g, \( U_{\text{cal}} = 86.5 \), \( z = -4.566 \), \( P < 0.001 \), two-tailed; Figure 1).

Infant mortality
Infant mortality rates for both sexes in the three ranks were as follows:

- **High ranking**:  
  - males: \( n = 62 \), 11.3%;
  - females: \( n = 50 \), 14.0%;

- **Middle ranking**:  
  - males: \( n = 33 \), 9.1%;
  - females: \( n = 31 \), 12.9%;

- **Low ranking**:  
  - males: \( n = 39 \), 17.9%;
  - females: \( n = 53 \), 18.9%.

The likelihood ratio calculated by logistic regression analysis showed that a fitted model was generated (Table 2). We found no independent variable with a significant effect on infant mortality. Among both high- and low-ranking mothers, infant mortality in Troop C was not sex biased, and dominance rank and the interaction between sex and dominance rank had no significant effects on infant mortality (Table 2).

Sex ratio at birth
The proportions of males born to the three ranks were as follows:

- **High ranking**: \( n = 133 \), 56.4%;
- **Middle ranking**: \( n = 98 \), 50.0%;
- **Low ranking**: \( n = 112 \), 46.4%.

Although the proportion of males born to low-ranking females was lower than those born to high-ranking females, the difference was not significant (Fisher’s exact test, \( P = 0.126 \), two-tailed).

Offspring sex and delivery rate in the subsequent year
Delivery rates in the subsequent year after the birth of sons or daughters in the three ranks were as follows:

- **High ranking**:  
  - after sons: \( n = 10 \), 30%;
  - after daughters: \( n = 9 \), 56%;

- **Middle ranking**:  
  - after sons: \( n = 7 \), 35%;
  - after daughters: \( n = 11 \), 35%;

- **Low ranking**:  
  - after sons: \( n = 6 \), 30%;
  - after daughters: \( n = 4 \), 20%.

The likelihood ratio calculated by logistic regression analysis showed that a fitted model was generated (Table 2). We found no independent variable with a significant effect on infant mortality. Among both high- and low-ranking mothers, infant mortality in Troop C was not sex biased, and dominance rank and the interaction between sex and dominance rank had no significant effects on infant mortality (Table 2).
middle ranking:
  after sons: \( n = 8, 13\% \); after daughters: \( n = 8, 0\% \);
low ranking:
  after sons: \( n = 8, 50\% \); after daughters: \( n = 11, 0\% \).
There was no significant difference in delivery rates after having reared a son or a daughter among high-ranking females (Fisher’s exact test, \( P = 0.370 \), two-tailed). However, note that, for low-ranking females, the delivery rate after rearing daughters was significantly lower than that after rearing sons (\( P = 0.018 \)).

Discussion

No bias of investment toward sons
In this study, Trivers and Willard’s and the LRC hypotheses were tested in provisioned, free-ranging Japanese macaques using a multivariate analysis and other statistical methods suitable when there is an abundance of controlled samples.

There was no sex difference in infant mortality and offspring body mass at 180 days of age, and delivery rates after rearing sons were not statistically lower than those after rearing daughters among females of high and low tripartite ranks. In addition, there was no significant difference in birth sex ratio between the two ranks. Thus, we found no statistically significant results for male-biased investment by mothers. High-ranking females, however, tended to have lower delivery rates in the subsequent year after rearing sons than after daughters and to produce sons at a higher rate than low-ranking females. These tendencies suggest that high-ranking Takasakiyama mothers invested more in sons than in daughters, although such a tendency was not found from analyses of infant body mass. A similar tendency was found in captive Japanese macaques transferred from Takasakiyama to Rome Zoo. According to Aureli et al. (1990), a significant male-biased birth sex ratio was found among high-ranking females, whereas this was not the case among middle- or low-ranking females.

Effects of maternal rank
Previous studies in Japanese macaques at Takasakiyama showed that high-ranking females obtained more digested energy than low-ranking females (Soumah and Yokota, 1991). As a result, high-ranking Takasakiyama females showed higher reproductive success, evaluated in terms of infant mortality, interbirth interval, and so on, than low-ranking females (Soumah and Yokota, 1992). In the present study, because high-ranking mothers reared heavier offspring than low-ranking females, it is likely that high-ranking females had a better nutritional condition than low-ranking females. Offspring of high-ranking mothers showed lower mortality rates than those of low-ranking mothers, although the difference was not statistically significant. These results can be interpreted that offspring of low-ranking mothers showed non-significant but higher mortality rates than those of high-ranking mothers because the body mass of offspring of low-ranking mothers was slightly heavier than the survival vs. death threshold of body mass.

Offspring survivorship and delay of subsequent reproduction
Although the reason for the low delivery rate in the subsequent year among low-ranking females after rearing daughters is unknown, it is unlikely that this low delivery rate was caused by an exaggerated nutritional investment in these daughters (Figure 1).

Delay of subsequent reproduction for low-ranking females after rearing daughters has been found for Barbary macaques, *M. sylvanus*, at Salem (Paul and Kuester, 1990) and rhesus macaques, *M. mulatta*, at Madingley (Gomendio, 1990). In the latter case, high levels of aggression and harassment based on local resource competition resulted in the delay of subsequent reproduction for low-ranking females with daughters (Gomendio et al., 1990). However, we found no evidence for intense LRC from the analyses of infant mortality and sex ratio at birth.

The markedly low delivery rate after rearing daughters and the lack of sex-biased infant mortality among low-ranking females suggest that these females increased their offspring’s chances of survival, irrespective of the offspring’s sex, postponing their own subsequent reproduction. From the viewpoint of lifetime reproductive success, for females, the offspring’s death is undoubtedly a greater loss than postponing the subsequent reproduction. Similarly, the increase in an offspring’s chance of survival with a delay in the subsequent delivery may operate in humans.

General discussion

Although this study examined sex differences in infant growth and mortality, birth sex ratio and delay of subsequent reproduction for the mothers of rearing sons or daughters, there are few primate populations for which relevant data have been presented. For a clear understanding of sex-biased maternal investment among primates, comparative studies of different populations, including provisioned and non-provisioned populations, are required. The difference in nutritional levels of animals between provisioned and non-provisioned populations may not be qualitative. For example, there is considerable overlap between the range of infant mortality rates in provisioned Japanese macaque populations (2.8–51.5%; Kurita, 2010) and that in non-provisioned populations (22.7–53.3%; Takahata et al., 1998). We need to objectively evaluate the amount of food and patterns of food distribution for both provisioned and non-provisioned populations and to use the above common indices to examine how sex-biased maternal investment differs among populations.

In humans, comparative studies of sex-biased parental investment among numerous tribes and/or countries should be conducted using common indices. These studies should use data not only on sex-biased parental investment but also on marriage system, property, dowry, the number of children per family, and other factors from reliable sources.

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References


