

## Female-Biased Maternal Investment in Rhesus Macaques

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### Key Words

Parental investment · Offspring sex · Dominance rank · Primates

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### Introduction

Parental investment theory predicts that parents should invest more in the offspring whose sex is less costly to rear and/or provides the higher fitness returns [1]. Differences in maternal dominance rank can, under certain circumstances, result in sex-biased investment. Trivers and Willard [2] argued that when variance in reproductive success (RS) is higher for males than for females and maternal investment has a higher impact on male RS than on female RS, high-ranking mothers should invest more in sons, and low-ranking mothers should invest more in daughters (male-quality hypothesis, or MQ). However, Clark [3] and Silk [4] suggested that, when females are philopatric and compete for resource, high-ranking mothers should invest more in daughters and low-ranking mothers should invest more in sons (local resource competition hypothesis, or LRC).

Although in some mammals there is good evidence of sex-biased investment in relation to maternal dominance rank [1], most studies of birth sex ratios and rank in cercopithecine monkeys produced no significant differences or contradictory results [5]. This pattern of findings may suggest that sex ratios in cercopithecines are subject to counteracting selective pressures, with either one prevailing on the other depending on the environmental circumstances [6]. The contradictory findings, however, could also be explained by the offspring survival hypothesis: whenever offspring mortality is significantly sex-biased, mothers should adjust birth sex ratios so as to maximize sex-specific offspring survival regardless of their dominance rank [7].

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This study was aimed at investigating sex-biased maternal investment in a large population of rhesus macaques (*Macaca mulatta*). The offspring survival hypothesis and the following predictions of the LRC hypothesis were tested: (1) offspring sex ratios at birth should be female biased for high-ranking mothers and male biased for low-ranking mothers; (2) interbirth intervals should be longer following daughters than following sons, especially for low-ranking mothers; (3) mortality should be female biased, and (4) daughter mortality should be higher for low-ranking than for high-ranking mothers. Although no predictions of the MQ hypothesis were specifically tested, many of them are opposite to those of the LRC hypothesis.

## Methods

Subject of this study was a population of 3,116 rhesus macaques living at the Field Station of the Yerkes Regional Primate Research Center in Lawrenceville, Ga., (USA). Reconstruction of the family trees of all individuals currently living in 10 large social groups produced a total of 57 matriline ranging in size from 9 to 190 individuals (mean  $\pm$  SEM = 54.67  $\pm$  5.05). Most matriarchs were wild caught in the mid-late 1960s and presumed to be unrelated. The 57 matriline included 671 reproductively active females (mean  $\pm$  SEM = 11.77  $\pm$  1.08 per matriline) and 3–7 generations (mean  $\pm$  SEM = 5.08  $\pm$  0.14 per matriline).

The groups were composed of 2–5 adult males and 15–35 adult females with their immature offspring. Females spent most of their life in their natal group whereas males were removed at the age of 4–5 years to reduce the probability of inbreeding. Adult males were rotated among groups every 3–4 years and new males were periodically introduced into the population. Information on sex of the infants (unknown in 51 cases), infant mortality in the first year, age at first successful reproduction for females and interbirth intervals was obtained from the colony records. Interbirth intervals were calculated considering only surviving (> 1 year) offspring and were recorded in terms of years. Information on dominance rank was obtained for 8 groups and 47 matriline. Dominance ranks were assessed on the basis of aggressive and submissive behavior recorded by different observers over the years. Adult females in the same matriline occupied adjacent positions in the group's dominance hierarchy and both individual and matriline rank were relatively stable over time. The analysis of matriline rank conducted here, however, has two limitations. First, although female members of each matriline typically lived in the same group, in some cases one or more individuals were removed from their family and later reintroduced in a different group. For analysis purposes, matriline rank was assigned in relation to the group that had most matriline members. Second, in some groups there was a matriline overthrow. After an overthrow, the second highest-ranking matriline usually rose to the top of the hierarchy while most members of the top-ranking matriline either died or had to be permanently removed. For analysis purposes, a top-ranking matriline was identified as the matriline that was at the top of the hierarchy in each group for the highest number of years. All the other matriline were identified as non-top ranking.

## Results

Top- and non-top-ranking matriline did not differ significantly in matriline size (mean  $\pm$  SEM: top = 74.25  $\pm$  14.19; non-top = 54.28  $\pm$  6.53; Mann-Whitney test:  $z = -1.6$ , n.s.), number of reproductively active females per matriline (top = 15.25  $\pm$  3.22; non-top: 11.56  $\pm$  1.39;  $z = -1.28$ , n.s.), sex ratio at birth (top = 44.85%; non-top = 47.07%;  $\chi^2 = 0.88$ , d.f. = 1, n.s.), infant mortality (top = 12.04%; non-top 11.52%;  $\chi^2 = 0.29$ ; d.f. = 1, n.s.), sex-biased infant mortality (top = 56.52%, non-top = 52.54%;  $\chi^2 = 3.20$ , d.f. = 1, n.s.), female age at first successful reproduction (top = 4.30  $\pm$  0.09 years;

non-top =  $4.42 \pm 0.45$ ;  $z = 0.82$ , n.s.), interbirth intervals (top =  $1.33 \pm 0.06$  years; non-top =  $1.41 \pm 0.05$ ;  $z = 0.48$ , n.s.), and interbirth intervals following sons and daughters (top, after sons =  $1.26 \pm 0.05$ ; after daughters =  $1.38 \pm 0.08$ ; non-top, after sons =  $1.28 \pm 0.04$ ; after daughters =  $1.50 \pm 0.07$ ; two-way ANOVA:  $F = 0.30$ , n.s.).

When data from all 57 matriline were pooled, offspring mortality in the first year of life was significantly male biased (male = 14.22% female = 10.45%;  $\chi^2 = 9.90$ , d.f. = 1,  $p = 0.001$ ). The sex ratio at birth was significantly female biased (46.27%; binomial test,  $z = -4.06$ ,  $p = 0.001$ ), and the interbirth intervals following the birth of surviving infants (>1 year) were significantly longer after a daughter than a son (daughter =  $1.48 \pm 0.06$  years; son =  $1.27 \pm 0.03$ ; t test for paired samples,  $t = 3.35$ ,  $n = 56$ ,  $p = 0.001$ ). Thus, mothers were more likely to skip a mating season after raising daughters than after sons.

## Discussion

In this large population of rhesus macaques, matriline rank did not significantly affect infant mortality, sex ratio at birth or any other measures of sex-biased maternal investment or RS considered in this study. It cannot be ruled out that some rank effects might have been masked by the methodological limitations in the assessment of matriline rank. Given the large sample size used in this study, however, if there had been a biologically meaningful effect of dominance rank on sex-biased maternal investment, this should have been apparent even with the methodological limitations of the data analysis. Thus, the findings of this study provide little support for either the LRC or the MQ hypothesis. In fact, only one prediction of the LRC hypothesis was empirically supported, namely that interbirth intervals following daughters are longer than those following sons [8, 9]. The finding that infant mortality was higher for males than for females is more consistent with the MQ than with the LRC hypothesis, and also with patterns of infant mortality in other polygynous mammals [1].

The results of this study provide strong support for the offspring survival hypothesis of sex-biased maternal investment [7]. The female-biased sex ratio at birth and the longer interbirth intervals following daughters indicate that maternal investment was significantly female-biased irrespective of dominance rank. Female-biased maternal investment could be an adaptive response to the lower mortality of daughters relative to sons. The reasons for higher mortality among male infants are not clear but may include higher vulnerability to disease or stress.

Along with other studies of macaques and baboons reporting that mothers overproduced the sex that was more likely to survive [7, 10], the present study supports the hypotheses that mothers can adaptively bias parental investment in relation to offspring sex and that sex-specific infant survival is a good predictor of biased birth sex ratios in cercopithecine monkeys.

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