

MATERNAL DOMINANCE RANK AND AGE AFFECT OFFSPRING SEX RATIO IN PIGTAIL MACAQUES

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This study tested some predictions of the local-resource-competition hypothesis and local-resource-enhancement hypothesis of sex-biased maternal investment in a population of pigtail macaques (*Macaca nemestrina leonina*). Offspring sex ratios in high- and low-ranking matriline were biased in opposite directions as predicted. Sex ratio in the middle-ranking matriline was female biased similar to the high-ranking matriline but became increasingly male biased with maternal age, similar to the low-ranking matriline. Interbirth intervals following surviving daughters were longer than those following sons, irrespective of rank, suggesting that daughters were more costly to rear than sons. Infant mortality was not significantly different for sons and daughters. The findings of this study are consistent with some, but not all, of the predictions of local-resource-competition and local-resource-enhancement hypotheses and suggest that middle-ranking mothers have specific investment strategies that change in relation to their age.

Key words: age, dominance rank, *Macaca nemestrina*, macaques, sex ratio

Parental investment theory predicts that parents should invest more in the offspring sex that is less costly to rear, provides the higher fitness returns, or both (Trivers 1985). In mammalian species with dominance hierarchies, maternal dominance rank is potentially an important source of sex-biased investment. It has been argued that when variance in reproductive success is higher for males than for females, and maternal investment can have a higher impact on male reproductive success than on female reproductive success, high-ranking mothers should invest more in sons, and low-ranking mothers should invest more in daughters (male-quality hypothesis—Trivers and Willard 1973). In species, however, where females are philopatric and compete intensely for resources, high-ranking mothers should invest more in daughters, and low-ranking mothers should invest more in sons (local-resource-competition hypothe-

sis—Clark 1978; Silk 1983). This should be particularly pronounced if mothers transmit their rank to their daughters and if high-ranking daughters enhance their matriline's access to local resources (local-resource-enhancement hypothesis—van Schaik and Hrdy 1991).

Sex-biased investment can take the form of biased sex ratio at birth or biased allocation of parental resources during the period of offspring dependence. Although in some mammals there is good evidence of both prenatal and postnatal sex-biased investment in relation to maternal dominance rank (Clutton-Brock 1991), studies of offspring sex ratios in cercopithecine monkeys have produced no significant differences or conflicting results (see Brown 2001 and Hiraiwa-Hasegawa 1993 for reviews). This pattern of findings has suggested 2 possible explanations: dominance rank has no effects on sex ratio at birth, and the significant findings reflect type I errors; or sex

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ratios in cercopithecines are subject to counteracting selective pressures, with either one prevailing over the other depending on environmental circumstances. Specifically, it has been argued that when competition for local resources is intense, the selective pressures hypothesized by the local-resource-competition model should prevail, whereas when there is little or no competition for resources, effects predicted by the male-quality hypothesis should be expressed (van Schaik and Hrdy 1991). To distinguish between these 2 alternatives, we need more studies from different species and populations, studies with larger sample sizes, and studies comparing species and populations living in different environments.

In addition to the 2 explanations mentioned previously, it is also possible that some discrepancies among findings of different studies have resulted from differences in methods, particularly in analysis of dominance rank. For example, some studies divided all female ranks into 2 classes, higher and lower (Altmann 1980; Meikle et al. 1984; Rhine 1994; Silk 1988; van Schaik et al. 1989); others used 3 rank classes, high, middle, and low (Berman 1988; Paul and Thommen 1984; Rawlins and Kessler 1986); others compared the top-ranking females with all the other females (Maestriperi 2001; Nevison et al. 1996; Simpson and Simpson 1982); and others used only matriarchs of high- and low-ranking matriline, excluding all other females from the analysis (Gomendio 1990). The reasons for choosing different classifications of rank were not always clear. Moreover, although middle-ranking individuals have often been included in the analysis, whether birth sex ratios should be significantly biased among these individuals and in which direction has not been explicitly discussed.

This study investigated sex ratios and other measures of maternal investment in pigtail macaques, thus contributing a new species and a new population to the data set

already available for cercopithecine monkeys. The main goal of the study was to test the following predictions of the local-resource-competition and local-resource-enhancement hypotheses: offspring sex ratios at birth should be female biased for high-ranking mothers and male biased for low-ranking mothers; offspring sex ratios should become increasingly male biased as a function of age in low-ranking mothers but not in high-ranking mothers; interbirth intervals should be longer following daughters than following sons, especially for low-ranking mothers; and infant mortality should be female biased, especially for low-ranking mothers (see van Schaik et al. 1989 for discussion of these hypotheses). Although no predictions of the male-quality hypothesis were specifically tested, many of them are complementary to those of the local-resource-competition and local-resource-enhancement hypotheses. Another aim of this study was to investigate sex-biased investment in middle-ranking females and assess whether these individuals were more similar to the high-ranking females or the low-ranking females in terms of birth sex ratios and other forms of sex-biased investment.

MATERIALS AND METHODS

Subject of this study was a population of 394 pigtail macaques (*Macaca nemestrina leonina*) living at the Field Station of the Yerkes Regional Primate Research Center in Lawrenceville, Georgia, over the last 30 years (5–7 generations). Reconstruction of matriline for about 50 living individuals showed that they were the descendants of 5 unrelated matriarchs that were caught in the wild and brought to the Center in the early 1960s, when the colony was first formed. The 5 matriline included 71 reproductively active females. In the first 5 years of the colony there were relatively few births, so most of the data are for individuals born in subsequent years. For most of the time, the pigtail macaques lived in 2 social groups (and more recently, in 1 group) housed in large outdoor–indoor compounds (25 by 25 m). Individual housing was limited to short periods during acute medical

treatment. Groups were composed of 2–5 adult males and 20–30 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 simulate the process of male migration and reduce the probability of inbreeding.

Information on sex of the infants (unknown in 23 cases), infant mortality in the 1st year, female age at parturition, and interbirth intervals were obtained from colony records. Infant mortality also included permanent removal of infants from their group because of injury. Causes of infant mortality or removal from the group in the 1st year have been analyzed in detail elsewhere (Maestriperi et al. 1997). Information on matriline dominance rank was obtained from long-term behavioral studies and derived from measures of aggression, submission, and displacement. Two matriline were classified as high ranking (size: 73 and 76 individuals), 1 as middle ranking (size: 113), and 2 as low ranking (size: 42 and 90). Similar to pigtail macaque populations in the wild (Caldecott 1987; Oi 1990), in the study population 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. Reliable information on matriline ranks was not available for the first 5–6 years after colony formation, but it was assumed that ranks were the same as in subsequent years. Statistical analyses included binomial tests, chi-square tests, and analyses of variance for repeated measures. Statistical tests were 2-tailed. Probabilities ≤ 0.05 were considered statistically significant.

RESULTS

Birth sex ratio in the whole population was 48.63% males (binomial test: $z = 0.47$, difference not significant). Birth sex ratios in the high- and middle-ranking matriline were female biased, whereas birth sex ratio in the low-ranking matriline was male biased (Fig. 1a), although differences were not significant. There was, however, an overall significant difference in birth sex ratios in relation to matriline rank ($\chi^2 = 10.76$, $d.f. = 2$, $P = 0.005$), with both high-ranking ($\chi^2 = 8.75$, $d.f. = 1$, $P < 0.01$) and middle-ranking matriline ($\chi^2 = 7.69$, $d.f.$

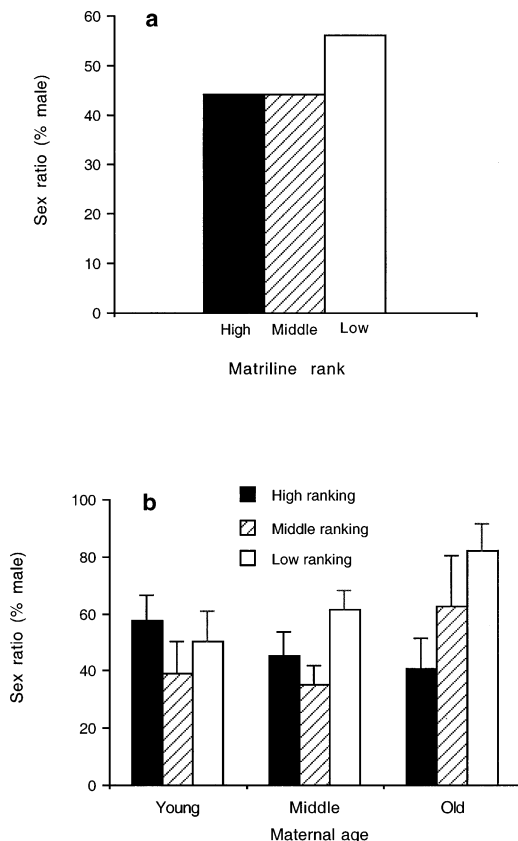


FIG. 1.—Sex ratios at birth in pigtail macaques as affected by social rank and age of mothers: a) birth sex ratios in high-ranking, middle-ranking, and low-ranking matriline and b) birth sex ratios for 3 categories of maternal age in high-ranking, middle-ranking, and low-ranking matriline. Bars indicate mean values; vertical lines indicate 1 SE.

$= 1$, $P < 0.01$) being significantly different from low-ranking matriline.

When birth sex ratios were analyzed in relation to 3 classes of maternal age (3–5, 5–12, and >12 years), analysis of variance did not reveal a main effect of age on birth sex ratios. There was, however, a significant interaction between age and matriline rank ($F = 3.90$, $d.f. = 4, 30$, $P = 0.01$) such that sex ratios became increasingly female biased with age in high-ranking matriline but increasingly male biased in middle- and low-ranking matriline (Fig. 1b).

Female age at 1st successful reproduction and total number of offspring were not significantly different in relation to matriline rank. Overall, infant mortality within the 1st year in the population was slightly female biased (46.98%; $z = 0.69$, difference not significant) and not affected by matriline rank or infant sex. Interbirth intervals following surviving daughters (mean number of years $\pm SE = 1.59 \pm 0.06$) were significantly longer than those following surviving sons (1.31 ± 0.10 ; $F = 5.47$, *d.f.* 1, 37, $P < 0.05$), irrespective of matriline rank or maternal age.

DISCUSSION

In this population of pigtail macaques, birth sex ratios in high- and low-ranking matrilines were biased in opposite directions: high-ranking matrilines produced more daughters than sons, whereas low-ranking matrilines produce more sons than daughters. Furthermore, maternal age had opposite effects on birth sex ratios in high- and low-ranking matrilines: sex ratios became increasingly female biased as a function of maternal age in the high-ranking matrilines, whereas the opposite was true for the low-ranking matrilines. Middle-ranking individuals showed a female-biased sex ratio similar to that of high-ranking individuals but with age effects on sex ratio similar to those in low-ranking individuals.

Differences in sex ratios in relation to maternal rank and age are generally consistent with the local-resource-competition and local-resource-enhancement hypotheses. High-ranking mothers invest more in the offspring that provides higher fitness benefits, as predicted by the local-resource-enhancement hypothesis, and increasingly overproduce daughters as they get older, perhaps because the competitive benefits associated with producing daughters increase with matriline size. In contrast, low-ranking mothers invest more in the offspring that is cheaper to rear, as predicted by the local-resource-competition hypothesis, and increasingly overproduce sons as

they get older, perhaps because their ability to invest in daughters and protect them from harassment further declines with their age.

The finding that patterns of sex ratio variation in middle-ranking matrilines are somewhat intermediate between those of high- and low-ranking matrilines may suggest that middle-rank matrilines are a heterogeneous class composed of both higher- and lower-ranking individuals. The findings of this study, however, are more consistent with the alternative hypothesis that middle-ranking matrilines are a homogeneous class of individuals who have different investment strategies in relation to their age. Middle-ranking females may invest more in daughters than in sons, like high-ranking females, when they are fully mature and their physical condition is optimal, and invest more in sons than in daughters, like low-ranking females, when they get older and their condition declines.

Infant mortality was not affected by infant sex or matriline rank (or both). Interbirth intervals following surviving daughters were longer than those following sons, suggesting that daughters were more costly to rear than sons. This finding is consistent with the local-resource-competition and local-resource-enhancement hypotheses and with previous results reported in other macaque species (Maestripiéri 2001; Paul and Thommen 1984; Silk 1988; Simpson and Simpson 1982; van Schaik et al. 1989). However, contrary to the predictions of the local-resource-competition and local-resource-enhancement hypotheses, dominance rank did not significantly affect interbirth intervals following daughters or sons. The higher costs of rearing daughters could result from the behavior of female infants, who spend more time near their mothers and suckling than male infants, or from behavior of their mothers, who reject suckling attempts by sons more than those by daughters (or both). In cercopithecine monkeys observations made during the first 2–3 months of infant life generally do not

indicate consistent differences in infant or maternal behavior in relation to sex, but such differences are known to emerge in subsequent months (Fairbanks 1996). Moreover, the costs of rearing daughters should progressively increase with their age because daughters will increasingly compete with their mothers for resources. Therefore, in macaques and other female philopatric species, daughters may be more costly to rear because their life histories lead them to spend, from early on, higher amounts of time near their mothers. Harassment by higher-ranking monkeys may increase the costs of rearing daughters for low-ranking mothers, as suggested by Silk (1983), but effects of harassment may be more evident in the wild, where competition for resources is harsher, than among food-provisioned monkeys (Dittus 1979).

Overall, the findings of this study lend support to the hypothesis that sex-biased parental investment observed in some populations of cercopithecine monkeys results from adaptive adjustment instead of stochastic processes. Specifically, the patterns of sex-biased investment observed among pigtail macaques are more consistent with predictions of the local-resource-competition and local-resource-enhancement hypotheses than with those of the male-quality hypothesis. This does not necessarily imply, however, that these hypotheses have more general validity for cercopithecine monkeys than does the male-quality hypothesis. Local variation in environmental circumstances can change the relationship between dominance rank and sex ratio (van Schaik and Hrdy 1991) or result in adaptive variation in sex ratio unrelated to dominance rank. For example, both wild and captive studies have shown that when infant mortality is strongly sex biased, mothers overproduce the offspring sex that is more likely to survive, regardless of their dominance rank (Maestriperi 2001; Wasser and Norton 1993). Offspring sex ratios are probably subject to selective pressures that act on different components of female reproductive

success, e.g., longevity and fertility versus offspring survival, and some components of female reproductive success may be less strictly associated with dominance rank than are others. Therefore, studies reporting no significant effects of maternal rank on birth sex ratio do not necessarily constitute evidence against the adaptive hypotheses. Future studies investigating dominance rank and sex ratio in monkeys, however, should further examine the investment strategies of middle-ranking individuals and take it into consideration that lumping these individuals with other rank classes can produce markedly different patterns of findings.

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