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Intensity of Local Resource Competition Shapes the Relationship between Maternal Rank and Sex Ratios at Birth in Cercopithecine Primates

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NOTES AND COMMENTS

INTENSITY OF LOCAL RESOURCE COMPETITION SHAPES THE
RELATIONSHIP BETWEEN MATERNAL RANK AND SEX RATIOS
AT BIRTH IN CERCOPITHECINE PRIMATES

According to sex ratio theory, parents should bias investment in offspring in line with expected reproductive returns from sons versus daughters (Hamilton 1967; Trivers and Willard 1973). In a more specific version, Trivers and Willard predict that mothers in good condition bias investment toward offspring of the sex most likely to benefit from the mother's advantaged situation. Because in polygynous species male fitness often depends more on size or condition than female fitness does, and because maternal investment influences offspring's adult size, this sex is usually, but not necessarily, male (Austad and Sunquist 1986; Clutton-Brock and Iason 1986; Hrdy 1987).

Social factors should also affect the sex ratio at birth: females high in dominance hierarchies should overproduce sons when they can endow them with greater prospects for growth and survival, thereby rendering them more competitive in the adult quest for mates. As predicted, high maternal rank is associated with male-biased sex ratios at birth as well as greater reproductive success for sons, but not daughters, in red deer (Clutton-Brock et al. 1984).

Studies of cercopithecine monkeys show a more complicated pattern. Several recent studies confirm the predictions of the Trivers-Willard hypothesis (Meikle et al. 1984; Paul and Kuester 1987, 1988; van Schaik et al. 1989): the proportion of males (PM) born to high-ranking females (PM_H) was significantly greater than the proportion of males born to low-ranking females (PM_L) in three species of macaque (*Macaca* spp.; see table 1, pt. A). Moreover, data on survival obtained in two of these populations indicate that mothers tend to overproduce the sex that is relatively more likely to survive (Meikle and Vessey 1988; van Schaik et al. 1989), suggesting that the shifts in sex ratio are adaptive.

These findings contrast with previous studies reporting the reverse pattern ($PM_H < PM_L$) for Amboseli baboons (*Papio cynocephalus*) and two species of macaque (M. J. A. Simpson and A. E. Simpson 1982; Altmann et al. 1988; Silk 1988; see table 1, pt. C). This pattern has been interpreted in terms of local resource competition (LRC; see Clark 1978) among females in female-philopatric species (Silk 1983, 1984). Other published studies find no significant effect of maternal rank on PM (Dunbar 1984; Wolfe 1984; Fedigan et al. 1986; Rawlins

TABLE 1

THE THREE DIFFERENT PATTERNS IN THE RELATIONSHIP BETWEEN MATERNAL RANK AND SEX RATIO AT BIRTH REPORTED FOR FEMALE-PHILOPATRIC CERCOPIHINE PRIMATES, INCLUDING ONLY STUDIES SHOWING SIGNIFICANT EFFECTS OR USING LARGE SAMPLES (> 200 BIRTHS)

Pattern and Species	Population and Period	PM _H	PM _L	No. of Births	G Adjusted (df = 1)	Sources
A. PM _H /PM _L > 1, supporting the Trivers-Willard hypothesis:						
<i>Macaca mulatta</i>	La Parguera, 1964-1978	.54	.49	719	2.0 ^a	Meikle et al. 1984
<i>M. sylvanus</i>	Affenberg Salem, 1978-1985	.55	.43	325	4.7*	Paul and Kuester 1987, 1988; J. Kuester, personal communication
<i>M. fascicularis</i>	Utrecht University, 1975-1987	.58	.43	213	4.4*	van Schaik et al. 1989
B. PM _H /PM _L = 1, supporting the null hypothesis of no rank effect:						
<i>M. mulatta</i>	California Primate Research Center, Davis, 1976-1985	.46	.54	374	2.4	Small and Hrdy 1986
<i>M. mulatta</i>	Cayo Santiago, 1974-1984 ^b	.51	.52	291	.0	Berman 1988
C. PM _H /PM _L < 1, supporting the local resource competition hypothesis:						
<i>Papio cynocephalus</i>	Amboseli, 1971-1983	.33	.63	80	7.0**	Altmann et al. 1988
<i>M. mulatta</i>	Madingley, 1960-1981	.28	.63	139	9.5**	Simpson and Simpson 1982
<i>M. radiata</i>	California Primate Research Center, 1971-1983	.49	.63	207	3.5 ^c	Silk 1988

^a Authors' test, using means of individual females, was significant at $P < .001$.

^b Figures given refer to highest- and lowest-ranking matriline in group; midranking matriline had PM = .32 ($n = 59$), significantly less than highest and lowest one.

^c $P = .06$, but effect was persistent through time.

* $P < .05$.

** $P < .01$.

and Kessler 1986; Small and Hrdy 1986; O'Brien and Robinson 1987; van Noordwijk and van Schaik 1987; Berman 1988; Cheney et al. 1988; see table 1, pt. B), and many more have probably remained unpublished owing to the absence of a significant rank effect. This array of outcomes is consistent with the following (null) hypothesis: rank has no effect on sex of progeny, and the few significant effects in either direction are Type I errors (Rawlins and Kessler 1986; Bernstein 1987).

In this note, we investigate the alternative possibility that the above patterns reflect adaptive responses molded by natural selection and that the variability arises because different processes predominate in different conditions. We begin by reviewing the assumptions of the local resource competition model and the evidence for it in group-living primates.

The LRC model, as expanded by Silk (1983, 1984), proposes that females should attempt to limit production of daughters born to other females where daughters remain in their natal group and compete there for limited resources. There is broad empirical support for this idea. First, in female-philopatric species, harassment of daughters, especially those born to low-ranking females, is common (Dittus 1979; Silk et al. 1981; Pereira 1988). Consequently, interbirth intervals following the birth of surviving infants are generally longer after daughters than after sons (Paul and Thommen 1984; A. E. Simpson and M. J. A. Simpson 1985; van Schaik et al. 1989; but see Berman 1988), and this effect is sometimes strongest among the low-ranking females (Gomendio et al. 1990). Second, mortality among immatures is female-biased in many unprovisioned populations (Dittus 1980; van Schaik and van Noordwijk 1983; Rhine et al. 1988; van Schaik and de Visser 1990). These sex differences contrast with the typical pattern among polygynous mammals in interbirth intervals (Clutton-Brock et al. 1982; Wolff 1988) and immature mortality (Clutton-Brock et al. 1985; Trivers 1985). Third, sex ratios at birth tend to be more male biased in female-philopatric than in non-female-philopatric primates (Johnson 1988). Fourth, in populations showing the rank effect on birth sex ratio predicted by the LRC model, daughters of high-ranking females tend to survive better relative to sons, while sons of low-ranking females tend to survive better relative to daughters (Altmann et al. 1988; Silk 1988), as predicted by the LRC model. This convergence of results suggests that LRC represents a powerful selective force in primate groups, which should be expected to affect birth sex ratios. However, we expect that both LRC and the more widely discussed Trivers-Willard effect operate simultaneously and that the degree to which either process is expressed depends on local conditions.

In female-philopatric populations with intense local resource competition, daughters appear to be a liability to low-ranking mothers but a benefit to high-ranking mothers (Altmann 1980). Cercopithecine daughters achieve positions in the hierarchy near their mothers and grow up to serve as allies in competition with other matriline. The larger the matriline, the more secure its status will be (Wrangham 1980; Dunbar 1988). Hence, cercopithecine daughters, perhaps especially high-ranking ones, enhance the matriline's access to local resources. Such "local resource enhancement" (LRE; a concept initially developed to explain male-biased sex ratios in birds with "helpers at the nest"; see Gowaty and

Lennartz 1985) leads parents to favor offspring of the sex whose cooperation enhances the lineage's access to food or mates or which enhances its ability to protect offspring. In this case, LRE operates as a subsidiary to LRC, generating similar predictions: high-ranking mothers should produce the philopatric sex.

Both the Trivers-Willard and LRC models can be subsumed under the general proposition that parents should invest more in the sex of offspring likely to yield the greatest number of grandchildren, and the previous discussion suggests that both models are plausible and could apply simultaneously to the same population. Hence, we should develop predictions that would tease apart their separate effects. First, however, we consider the case in which they predict the same patterns, in order to assess the power of these models. In male-bonded species such as spider monkeys (*Ateles* spp.) and chimpanzees (*Pan troglodytes*), males forge alliances with locally available males (usually kin) to patrol access to females in a community, protecting these females and their offspring from males in neighboring communities. Since outcast males have been observed, the membership of the male alliance may be limited and mothers may compete to ensure their sons' access to it (Kawanaka 1984; Goodall 1986; Symington 1987). Male-biased infanticide reported for chimps may similarly be interpreted as attempts by adult males to limit recruitment of distantly related males (Hiraiwa-Hasegawa 1987). Hence, in such species the effects predicted by LRC (or LRC linked with LRE) and Trivers-Willard would be mutually reinforcing. This view derives support from one population of spider monkeys (*A. paniscus*) where only high-ranking females produced sons, and low-ranking females specialized in the production of daughters (Symington 1987).

In female-philopatric species, both the LRC and Trivers-Willard models predict that the effect of rank on sex ratios at birth should become more pronounced as resources become scarce and competition for them becomes more intense, but with a crucial difference. According to Trivers-Willard, it should be increasingly difficult for low-ranking mothers to produce competitive sons (cf. red deer in Clutton-Brock et al. [1985]), so they should respond to local resource competition by producing relatively fewer sons. By contrast, LRC predicts that under the same conditions of scarcity, low-ranking mothers would find it difficult to protect daughters. This is consistent with patterns in juvenile mortality among female-philopatric primates. With provisioning, males and females die at equal rates, but in wild populations, mortality is higher among females (van Schaik and de Visser 1990). Local resource competition predicts that low-ranking females will produce relatively fewer daughters as resources become scarce. Hence, by examining the relationship between a female's rank and her birth sex ratio as a function of resource availability, we can distinguish between the two models.

Unfortunately, direct measures of the intensity of competition for local resources are not currently available, so we must use an indirect measure: annual population growth. We assume that availability of resources, particularly food, but also secure refuges and the tension-reducing proximity of allies rather than competitors, affects the fertility of mothers as well as the survival and growth of immatures. This process in turn determines population growth. The advantage of this indirect measure is that data on crude annual growth rate are available for

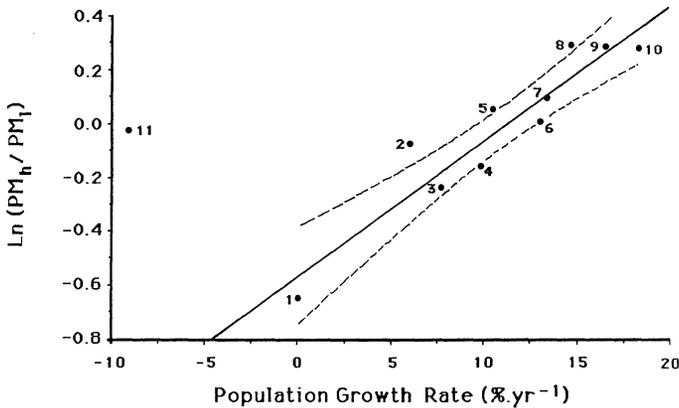


FIG. 1.—The relationship between local resource competition (estimated through crude annual growth rate of the population, in %) and the effect of maternal rank on the sex ratio at birth (as measured by the natural logarithm of PM_H/PM_L) in female-bonded cercopithecines. The following studies were included (n refers to number of sexed infants born to mothers of known rank): 1. *Papio cynocephalus*, wild, $n = 80$, Altmann et al. 1988; 2. *Macaca fascicularis*, wild, $n = 98$, van Noordwijk and van Schaik 1987, and C. P. van Schaik, unpublished data, for population growth; 3. *M. radiata*, captive, $n = 207$, Silk 1988, and J. B. Silk, personal communication, for population growth; 4. *M. mulatta*, captive, $n = 374$, Small and Hrdy 1986, population growth calculated from Smith 1982; 5. *M. arctoides*, captive, $n = 91$, Nieuwenhuijsen 1985; 6. *M. mulatta*, free-ranging, $n = 291$ (Berman [1988] reported three rank classes; here results of medium-rank mothers are divided equally between high- and low-ranking ones). Population growth is from Rawlins and Kessler 1986; 7. *M. mulatta*, free-ranging, $n = 719$, Meikle et al. 1984; 8. *M. fuscata*, zoo, $n = 85$, Aureli et al. 1990, and F. Aureli, personal communication, for growth; 9. *M. fascicularis*, captive, $n = 213$, van Schaik et al. 1989, and C. P. van Schaik, unpublished data on growth; 10. *M. sylvanus*, free-ranging, $n = 325$, Paul and Kuester 1987, 1988; and 11. *Cercopithecus aethiops*, wild, $n = 73$, Cheney et al. 1988.

many populations on which we have data on maternal rank and sex ratios. The disadvantage is of course that these growth rates might be distorted by factors unrelated to resource competition, such as human interference, infectious diseases, or predation.

Direction and strength of rank effects on birth sex ratio are expressed in a single measure, $\ln(PM_H/PM_L)$. Figure 1 shows the positive relationship between population growth rate and $\ln(PM_H/PM_L)$ for all female-philopatric primate populations for which both variables are known ($r = 0.620$, $n = 11$, $P < .05$). However, figure 1 contains an outlier, point 11, from a population of vervet monkeys in Amboseli, Kenya (*Cercopithecus aethiops*; see Cheney et al. 1988), with a very negative growth rate (-9.0%) but only a slightly negative $\ln(PM_H/PM_L)$. In fact, this point is more than 10 SD away from the regression line through the other 10 points and well outside the (extrapolated) confidence limits of estimated values of $\ln(PM_H/PM_L)$. Field workers attribute the decline to recent habitat changes (Cheney et al. 1988). If outlying point 11 is excluded, the relationship is very tight ($r = 0.941$, $n = 10$, $P < .001$). This is not an artifact of systematic variation in the population's PM and the birth rate of one class relative to the

other since both PM_H and PM_L are strongly correlated with population growth ($r = +0.81$, $n = 10$, $P < .01$, and $r = -0.88$, $P < .001$, respectively; point 11 is excluded) and the population's PM is not ($r = -0.13$, NS).

This result suggests that female-philopatric cercopithecines are subject to counteracting selective pressures on sex allocation with the result that rank effects on sex ratios can go in either direction, depending on conditions. When competition for local resources is intense, the selective pressures hypothesized by the LRC model take priority in determining the sex ratio pattern; that is, LRC overwhelms other effects. Only when competition is relaxed are the effects hypothesized by Trivers and Willard expressed. This indicates that whenever group-living polygynous or promiscuous mammals show female philopatry and matrilineal inheritance of rank, the ability to support daughters brings greater fitness rewards than the ability to produce more viable sons. In order to evaluate this interpretation, we need direct estimates of the maternal effect on the growth, development, and survival (cf. Gomendio et al. 1990) and lifetime reproductive success of primate sons and daughters and, in particular, observations of the social mechanisms involved in a range of socioecological conditions. At any rate, this result supports the idea that female cercopithecines really do adjust their birth sex ratios, even though the physiological mechanisms involved (James 1987) remain mysterious.

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LITERATURE CITED

- Altmann, J. 1980. Baboon mothers and infants. Harvard University Press, Cambridge, Mass.
- Altmann, J., G. Hausfater, and S. A. Altmann. 1988. Determinants of reproductive success in savannah baboons, *Papio cynocephalus*. Pages 403–418 in T. H. Clutton-Brock, ed. Reproductive success. University of Chicago Press, Chicago.
- Aureli, F., G. Schino, C. Cordischi, R. Cozzolini, S. Scucchi, and C. P. van Schaik. 1990. Social factors affect the secondary sex ratio in captive Japanese macaques. *Folia Primatologica* 55:176–180.
- Austad, S., and M. E. Sunquist. 1986. Sex-ratio manipulation in the common opossum. *Nature* 324:58–60.
- Berman, C. M. 1988. Maternal condition and offspring sex ratio in a group of free-ranging rhesus monkeys: an eleven-year study. *American Naturalist* 131:307–328.
- Bernstein, I. S. 1987. The evolution of nonhuman primate social behavior. *Genetica* 73:99–116.
- Cheney, D. R., R. M. Seyfarth, S. J. Andelman, and P. C. Lee. 1988. Reproductive success in vervet monkeys. Pages 384–402 in T. Clutton-Brock, ed. Reproductive success. University of Chicago Press, Chicago.
- Clark, A. B. 1978. Sex ratio and local resource competition in a prosimian primate. *Science* (Washington, D.C.) 201:163–165.
- Clutton-Brock, T. H., and G. R. Iason. 1986. Sex ratio variation in mammals. *Quarterly Review of Biology* 61:339–374.
- Clutton-Brock, T. H., F. E. Guinness, and S. D. Albon. 1982. Red deer, behavior and ecology of two sexes. University of Chicago Press, Chicago.

- Clutton-Brock, T. H., S. D. Albon, and F. E. Guinness. 1984. Maternal dominance, breeding success, and birth sex ratios in red deer. *Nature* (London) 308:358–360.
- . 1985. Parental investment and sex differences in juvenile mortality in birds and mammals. *Nature* (London) 313:131–133.
- Dittus, W. P. J. 1979. The evolution of behaviors regulating density and age-specific sex ratios in a primate population. *Behaviour* 69:265–302.
- . 1980. The social regulation of primate populations: a synthesis. Pages 263–286 in D. Lindburg, ed. *The macaques*. van Nostrand, New York.
- Dunbar, R. I. M. 1984. *Reproductive decisions*. Princeton University Press, Princeton, N.J.
- . 1988. *Primate social systems*. Cornell University Press, Ithaca, N.Y.
- Fedigan, L. M., L. Fedigan, S. Gouzoules, and H. Gouzoules. 1986. Lifetime reproductive success in female Japanese macaques. *Folia Primatologica* 47:143–157.
- Gomendio, M., T. H. Clutton-Brock, S. D. Albon, F. E. Guinness, and M. J. Simpson. 1990. Mammalian sex ratios and variation in costs of rearing sons and daughters. *Nature* 343:261–263.
- Goodall, J. 1986. *The chimpanzees of Gombe*. Belknap, Cambridge, Mass.
- Gowaty, P., and M. R. Lennartz. 1985. Sex ratios of nestling and fledgling red-cockaded woodpeckers (*Picoides borealis*). *American Naturalist* 126:347–353.
- Hamilton, W. D. 1967. Extraordinary sex ratios. *Science* (Washington, D.C.) 156:477–488.
- Hiraiwa-Hasegawa, M. 1987. Infanticide in primates and a possible case of male-biased infanticide in chimpanzees. Pages 125–139 in Y. Ito, J. L. Brown, and J. Kikkawa, eds. *Animal societies: theories and facts*. Japan Scientific Societies, Tokyo.
- Hrdy, S. B. 1987. Sex-biased parental investment among primates and other mammals: a critical evaluation of the Trivers-Willard hypothesis. Pages 97–147 in R. Gelles and J. Lancaster, eds. *Child abuse and neglect: biosocial dimensions*. Aldine, New York.
- James, W. H. 1987. The human sex ratio. Part 2: A hypothesis and a program of research. *Human Biology* 59:873–900.
- Johnson, C. N. 1988. Dispersal and the sex ratio at birth in primates. *Nature* 332:726–728.
- Kawanaka, K. 1984. Association, ranging, and the social unit in chimpanzees of the Mahale Mountains, Tanzania. *International Journal of Primatology* 5:411–434.
- Meikle, D. B., and S. H. Vessey. 1988. Maternal dominance rank and lifetime survivorship of male and female rhesus monkeys. *Behavioral Ecology and Sociobiology* 22:379–383.
- Meikle, D. B., B. L. Tilford, and S. H. Vessey. 1984. Dominance rank, secondary sex ratio and reproduction of offspring in polygynous primates. *American Naturalist* 124:173–188.
- Nieuwenhuijsen, K. 1985. *Geslachtshormonen en gedrag bij de beermaakak*. Ph.D. thesis. Erasmus University, Rotterdam.
- O'Brien, T. G., and J. G. Robinson. 1987. The effects of group size and female rank on sex ratio at birth in capuchins, *Cebus olivaceus*. *International Journal of Primatology* 8:499.
- Paul, A., and J. Kuester. 1987. Dominance, kinship and reproductive value in female barbary macaques (*Macaca sylvanus*) at Affenberg Salem. *Behavioral Ecology and Sociobiology* 21:323–331.
- . 1988. Life-history patterns of barbary macaques (*Macaca sylvanus*) at Affenberg Salem. Pages 199–228 in J. E. Fa, ed. *Ecology and behavior of food-enhanced primate groups*. A. Liss, New York.
- Paul, A., and D. Thommen. 1984. Timing of birth, female reproductive success and infant sex ratio in semifree-ranging barbary macaques (*Macaca sylvanus*). *Folia Primatologica* 42:2–16.
- Pereira, M. E. 1988. Agonistic interactions of juvenile savanna baboons. *Ethology* 79:195–217.
- Rawlins, R. G., and M. J. Kessler. 1986. Secondary sex-ratio variation in the Cayo Santiago macaque population. *American Journal of Primatology* 10:87–99.
- Rhine, R. J., S. K. Wasser, and G. W. Norton. 1988. Eight-year study of social and ecological correlates of mortality among immature baboons of Mikumi National Park, Tanzania. *American Journal of Primatology* 16:199–212.
- Silk, J. B. 1983. Local resource competition and facultative adjustment of sex ratios in relation to competitive abilities. *American Naturalist* 121:56–66.
- . 1984. Local resource competition and the evolution of male-biased sex ratios. *Journal of Theoretical Biology* 108:203–213.

- . 1988. Maternal investment in captive bonnet macaques (*Macaca radiata*). *American Naturalist* 132:1–19.
- Silk, J. B., C. Clark-Wheatley, P. Rodman, and A. Samuels. 1981. Differential reproductive success and facultative adjustment of sex ratios among captive female bonnet macaques (*Macaca radiata*). *Animal Behaviour* 29:1106–1120.
- Simpson, A. E., and M. J. A. Simpson. 1985. Short-term consequences of different breeding histories for captive rhesus macaque mothers and young. *Behavioral Ecology and Sociobiology* 18:83–89.
- Simpson, M. J. A., and A. E. Simpson. 1982. Birth sex ratios and social rank in rhesus monkey mothers. *Nature* 300:440–441.
- Small, M. F., and S. B. Hrdy. 1986. Secondary sex ratios by maternal rank, parity, and age in captive rhesus macaques (*Macaca mulatta*). *American Journal of Primatology* 11:359–365.
- Smith, D. G. 1982. A comparison of the demographic structure and growth of free-ranging and captive groups of rhesus monkeys (*Macaca mulatta*). *Primates* 23:24–30.
- Symington, M. M. 1987. Sex ratio and maternal rank in wild spider monkeys: when daughters disperse. *Behavioral Ecology and Sociobiology* 20:421–425.
- Trivers, R. L. 1985. *Social evolution*. Benjamin Cummings, Menlo Park, Calif.
- Trivers, R. L., and D. E. Willard. 1973. Natural selection of parental ability to vary the sex ratio of offspring. *Science (Washington, D.C.)* 179:90–92.
- van Noordwijk, M. A., and C. P. van Schaik. 1987. Competition among female long-tailed macaques (*Macaca fascicularis*). *Animal Behaviour* 35:577–589.
- van Schaik, C. P., and J. A. G. M. de Visser. 1990. Fragile sons or harassed daughters? Sex differences in mortality among juvenile primates. *Folia Primatologica* 55:10–23.
- van Schaik, C. P., and M. A. van Noordwijk. 1983. Social stress and the sex ratio of neonates and infants among non-human primates. *Netherlands Journal of Zoology* 33:259–265.
- van Schaik, C. P., W. J. Netto, A. J. J. van Amerongen, and H. Westland. 1989. Social rank and sex ratio of captive long-tailed macaque females (*Macaca fascicularis*). *American Journal of Primatology* 19:147–161.
- Wolfe, L. D. 1984. Female rank and reproductive success among Arashiyama B Japanese macaques (*Macaca fuscata*). *International Journal of Primatology* 5:133–143.
- Wolff, J. O. 1988. Maternal investment and sex ratio adjustment in American bison calves. *Behavioral Ecology and Sociobiology* 23:127–133.
- Wrangham, R. W. 1980. An ecological model of female-bonded primate groups. *Behaviour* 75:262–299.

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