Behav Ecol Sociobiol (1988) 22:379–383

Behavioral Ecology and Sociobiology

Maternal dominance rank and lifetime survivorship of male and female rhesus monkeys

Douglas B. Meikle[1] **and Stephen H. Vessey**[2]

[1] Department of Biology, Hood College, Frederick, MD 21701, USA
[2] Department of Biology, Bowling Green State University, Bowling Green, OH 43403, USA

Received May 11, 1987 / Accepted February 5, 1988

Summary. The longitudinal survivorship of a group of free-ranging male and female rhesus monkeys from La Parguera, Puerto Rico, was analyzed. Males had lower age-specific survivorship than females. There were no differences in the survivorship of daughters of high- and low-ranking mothers and there was no correlation between total number of offspring born and maternal rank for females. However, the sons of low-ranking mothers had lower survivorship than the sons of high-ranking females. This sex-related difference in survivorship, in conjunction with other evidence, indicates that the average lifetime reproduction of sons of low-ranking females is lower than that of daughters and vice versa for offspring of high-ranking females.

Introduction

There are two models that predict different relationships between maternal dominance ranks and the survivorship and reproduction of males and females in polygynous primate species (Trivers and Willard 1973; Altmann 1980; Silk 1983). First, Trivers and Willard (1973) hypothesized that in polygynous species, since the variance in the reproduction of males is greater than that of females, then the "condition" (e.g., social dominance ranks) of mothers may have a greater influence on the development and reproduction of sons than daughters. The second model hypothesized that since males have their mothers' ranks only until they emigrate from their natal groups, but daughters remain to have their mothers' dominance ranks for life, then the competitive abilities and reproduction of daughters vary more with maternal rank than that of sons (Altmann 1980; Silk 1983).

These two models make opposite predictions about the relationships between maternal dominance ranks and the lifetime reproduction of male and female offspring, but there are very few data that bear on these relationships for primates (Clutton-Brock and Albon 1982). One difficulty in collecting such data is that one needs to know the average lifetime reproduction for all sons and daughters born to females of different ranks, not just the reproduction of those that reach sexual maturity. Here we present the first longitudinal analysis of survivorship for free-ranging rhesus monkeys and discuss how patterns of survivorship may influence their reproduction.

Methods

The subjects of this study were born on La Cueva Island at La Parguera, Puerto Rico (Vandenbergh 1967). The animals were supplied ad libitum with water and commercial monkey food at feeders throughout the island. Each monkey received an identification tattoo during its first year, and maternal relations were known for nearly all animals (Vandenbergh 1967; Drickamer 1974; Meikle et al. 1984). The colony was censused frequently (usually daily) by technicians and investigators.

We present data for two groups: all males ($N=44$) and all females ($N=43$) born in the three original social groups, A, C and E, during the five-year period from 1964–1968. For longitudinal analyses we exclude five females that were not moved with the rest of the La Parguera colony to Morgan Island, S.C., in 1980. Three low-ranking and three high-ranking female subjects (14%) were alive and moved to Morgan Island. One low-ranking and three high-ranking male subjects (9%) were alive, but not moved to Morgan Island, so we follow males only until 1980 and females until 1985. Hence, we were able to follow over 86% of females and over 90% of males through their complete lifespan.

Table 1 shows the numbers of males and females born during each year of the five year sample period as well as how many mothers produced one, two, three or four subjects. The male subjects were produced by a total of 29 mothers, comprising 23 different genealogies while the female subjects were produced by a total of 23 mothers comprising 21 different genealogies. There were no significant differences in the number of

Table 1. **a** Number of male and female births for each year of the five year sample period. **b** Number of mothers that gave birth to one, two, three or four of the male and female subjects

	a Year born					Total
	1964	1965	1966	1967	1968	
Males	6	8	9	11	10	44
Females	6	4	10	10	13	43
Total	12	12	19	21	23	87

		b Number of subjects born per female			
		1	2	3	4
Mothers of	males	16	11	2	0
	females	8	11	3	1

high- and low-ranking mothers that produced one, two, three or four of the male ($\chi^2_3=0.51$, $P>0.1$) or female ($\chi^2_3=0.68$, $P>0.1$) subjects.

Dominance ranks were based on the outcome of agonistic encounters (Sade 1967). The original females established dominance ranks and the families (genealogies) they produced shared those ranks. We observed over 5,000 agonistic encounters between members of different genealogies during 1965–1971 and 1977–1980 and we constructed dominance matrices for genealogies so that a linear ranking could be achieved (Wilson 1981; Boyd and Silk 1983). Genealogical dominance ranks did not change during the colony's history, which also was the case for rhesus monkeys on Cayo Santiago (Sade et al. 1977).

Results

The proportion of males that died each year was more frequently greater (11 of 15 years, with one tie) than the proportion of females that died each year ($P<0.03$, sign test; Siegel 1956). This sex difference in mortality was particularly large during the first two years of life, with 57% (25/44) of males and 35% (15/43) of females dying during the first two years ($\chi^2_1=4.21$, $P<0.05$). In addition, of those reaching sexual maturity, 44% (7/16) of the males died and only 9% (2/22) of the females died during the three years past maturity ($\chi^2_1=6.16$, $P<0.02$).

The sexes also differed with respect to the relationship between survivorship and maternal rank. There was a large difference in the survivorship of sons of high- and low-ranking females (Fig. 1a, Table 2). During the first year of life more sons of low-ranking females died (64%) than sons of high-ranking females (27%, $\chi^2_1=5.87$, $P<0.02$). The rank-related difference in survivorship of sons of high- and low-ranking females that was established during the first year increased slightly by the sixth year (59% and 86% having died respectively), by which age more than 95% of males had emigrated from their natal groups and some had become members in other nonnatal groups. The sons of low-ranking females tended to have greater age specific mortality compared to the sons of high-ranking females, and as a result, the lifespans of males were positively correlated with their mothers' ranks (Kendall tau, corrected for ties = 0.233, $P<0.05$). There was no relationship between the ages and ranks of the mothers of subjects, so the rank-related pattern of mortality among males was not a result of differences in maternal age (Meikle et al. 1984).

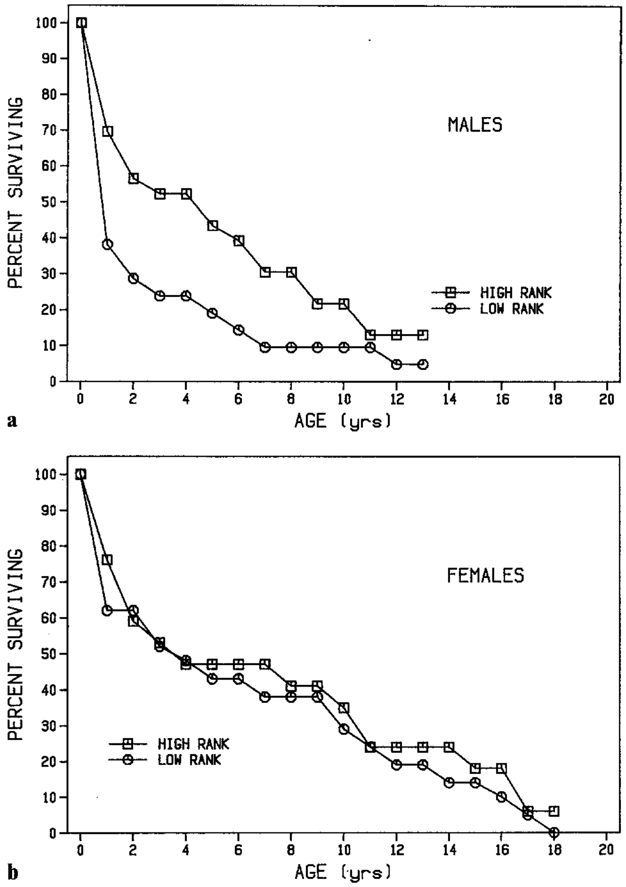

Fig. 1a, b. Percent of **a** males and **b** females surviving to each age in relation to maternal rank

In contrast to the pattern of mortality among males, there were no differences in the survivorship of daughters of high- and low-ranking mothers (Fig. 1b, Table 2). Accordingly, there was not a significant correlation between maternal rank and lifespan for females (Kendall tau, corrected = 0.14, $P>0.1$). There also was not a significant correla-

Table 2. A comparison of the proportion of individuals dying each year for the sons and daughters of high- and low-ranking females

		Sons		Daughters	
Age dead	Rank *n*	High (22)	Low (22)	High (17)	Low (21)
0– 1		0.27	0.64	0.24	0.33
1– 2		0.19	0.25	0.23	0.07
2– 3		0.15	0.17	0.10	0.15
3– 4		0.0	0.0	0.11	0.09
4– 5		0.09	0.20	0.0	0.10
5– 6		0.10	0.25	0.0	0.0
6– 7		0.22	0.33	0.0	0.11
7– 8		0.0	0.0	0.13	0.0
8– 9		0.29	0.0	0.0	0.0
9–10		0.0	0.0	0.0	0.0
10–11		0.40	0.50	0.14	0.25
11–12		0.0	0.0	0.33	0.17
12–13		0.0	b	0.0	0.20
13–14		0.0	–	0.0	0.0
14–15		a	–	0.0	0.25
15–16		–	–	0.25	0.0
16–17		–	–	0.0	0.33
17–18		–	–	0.50	0.67
18–19		–	–	c	d

Letters denote animals still living at end of study: a = 3, b = 1, c = 3, d = 2

tion between the lifetime production of offspring by females and the ranks of their mothers (Kendall's tau, corrected = 0.09, $P > 0.1$). In a separate analysis (Meikle et al. 1984) of the number of offspring produced per reproductive year by females at the La Parguera colony, high-ranking females showed a small (7%), but significantly greater production of offspring than low-ranking females. However, this difference is much smaller than the rank-related difference in the mortality and probable reproduction of sons.

Although we could not record the reproduction of males directly, the pattern of mortality in this study indicates that sons born to high-ranking females have a much higher probability of reproducing than do sons born to low-ranking females. Sons of high-ranking females were 2–3 times more likely to survive to sexual and social maturity, and this difference persisted throughout their lifespans. Therefore, if all else is equal among mature males, the reproduction of sons of high-ranking females is greater than that of sons of low-ranking females.

Discussion

It would take a large advantage in the reproduction of the mature sons of low-ranking females to make up for the influence of prepubertal mortality on their average lifetime reproduction, compared to the sons of high-ranking females. However, evidence suggests that the reproductive success of the mature sons of high-ranking females is greater than that of the mature sons of low-ranking females, making the actual disparity in reproduction even greater than that established by differential mortality among immature males. Sons of high-ranking females are more frequently members in high-ranking nonnatal groups, remain longer in those groups (Meikle et al. 1984), and thus attain higher rank (Drickamer and Vessey 1973) than do sons of low-ranking females.

Staying longer in nonnatal groups allows sons of high-ranking females to father offspring during more breeding seasons, to accrue tenure and rank, and to protect those offspring better and longer than can the sons of low-ranking females (Bernstein 1976). Taken together, these data suggest that the average lifetime reproduction of sons of low-ranking females is much lower than that of the sons of high-ranking females, while a much weaker rank-related difference exists in the lifetime reproduction of daughters.

The rank-related difference in the reproduction of male rhesus monkeys leads to the prediction that mothers invest differentially in sons and daughters in relation to their ranks (Trivers and Willard 1973). This prediction was fulfilled by the secondary sex ratios at the La Parguera colony: high-ranking females gave birth to more sons than daughters and low-ranking females gave birth to more daughters than sons (Meikle et al. 1984).

The disproportionately high mortality of sons of low-ranking females may have resulted from agonistic encounters with other animals. Silk et al. (1981) reported that females that lived to one month had greater mortality than juvenile males in a captive group of bonnet macaques (*M. radiata*), and that much of this mortality was related to agonistic encounters among females. However, of all infants born, the sons of low-ranking females had lower survivorship than both daughters of low-ranking females and sons of high-ranking females (Silk et al. 1981; Silk 1983), similar to the pattern we observed in our colony.

The cause of death for most of our subjects was not known. We have occasional field note records of wounding, but most animals simply were no longer observed in their group and were later found dead and partially decomposed. In many instances, animals had decomposed to the extent that they could not be identified. Our assumption that individuals that disappeared had died was corroborated by the nearly exact correspondence between the numbers of carcasses found and individuals that disappeared.

The relatively high mortality of immature sons of low-ranking females on La Cueva may have resulted from decreased investment by mothers (Trivers and Willard 1973), particularly during the first year, when maternal investment is greatest (Berman 1980; Vessey and Meikle 1984). Such adjustment of investment might have involved a reduction in the risks that low-ranking females took to protect their sons. Reduced protection may result in higher levels of wounding, stress (Chamove and Bowman 1976), and increased suceptibility to disease (Christian 1980). Although we do not have data on the cause of death for all subjects, 15 of these subjects also were subjects of focal observations in a study of mother-infant interactions during the first year of life (Vessey and Meikle 1984). The three sons of low-ranking females in that sample died from an infection (probably *Shigella*) of the jaw during the first year (unpublished data from Vessey and Meikle 1984).

The explanation that disproportionate mortality of immature males results from adaptive variation in maternal investment (i.e., the Trivers-Willard model) is sometimes contrasted with the explanation that such mortality occurs because males simply are more vulnerable than females to certain environmental circumstances (Clutton-Brock et al. 1985; Hrdy 1987). It should be noted, however, that if males are "simply" more vulnerable than females and, as a result, the sons of low-ranking females have higher mortality and therefore lower average lifetime reproductive success than sons of high-ranking females, then selection will favor decreased prenatal investment in sons by low-ranking females. Hence the prediction of variation in the secondary sex ratio holds whether the differential mortality is caused by rank-related maternal investment or is simply a passive effect of maternal rank. The crucial point is whether there is a difference in the average lifetime reproduction of one sex or the other that is consistently related to some condition of parents.

Clutton-Brock et al. (1985) have argued that the higher mortality of male than female immatures in polygynous bird and mammal species is related to the higher growth rates and larger sizes of males which make them susceptible to reduced maternal ability to provide nutrition. Differences in maternal ability to provide nutrition is not a likely explanation for the rank-related mortality that we observed among males, since our colony was provisioned ad libitum.

Differences in the mortality of males and females after sexual maturation are expected for a polygynous species such as *Macaca mulatta* since adult males emigrate from their natal groups (Lindburg 1969; Drickamer and Vessey 1973) and are frequently involved in dangerous agonistic encounters (Sade et al. 1977; Alexander et al. 1979; Clutton-Brock et al. 1985). However, only a detailed analysis of the interactions between immatures and their mothers, relatives, and unrelated animals will yield information about the maternal rank-related pattern of mortality of rhesus monkeys prior to sexual maturity.

Acknowledgements. We gratefully acknowledge the support of the Caribbean Primate Research Center (FDA contract 223-74-1024 and NIH contract No1-RR-7-2115), Litton Bionetics and Organon Technika. In addition, we thank T.H. Clutton-Brock, J. Commito, H.J. Herbert, S. Meikle, T. Methany, D. Taub, and K. Vessey for invaluable comments and assistance.

References

Alexander RD, Hoogland JL, Howard RD, Noonan KM, Sherman PW (1979) Sexual dimorphism and breeding systems in pinnipeds, ungulates, primates and humans. In: Chagnon NA, Irons W (eds) Evolutionary biology and human social behavior: an anthropological perspective. Duxbury Press, North Scituate, MA, pp 402–435

Altmann J (1980) Baboon mothers and infants. Harvard University Press, Cambridge, MA

Berman C (1980) Mother-infant relationships among free-ranging rhesus monkeys on Cayo Santiago: a comparison with captive pairs. Anim Behav 28:860–873

Bernstein IS (1976) Dominance, aggression and reproduction in primate societies. J Theor Biol 60:459–472

Boyd R, Silk JB (1983) A method for assigning cardinal dominance ranks. Anim Behav 31:45–58

Chamove AS, Bowman RE (1976) Rank, rhesus social behavior and stress. Folia Primatol 26:57–66

Christian JJ (1980) Endocrine factors in population regulation. In: Cohen MN, Malpass RS and Klein HG (eds) Biosocial mechanisms of population regulation. Yale University Press, New Haven, pp 55–115

Clutton-Brock TH, Albon SD (1982) Parental investment in male and female offspring in mammals. In: King's College Sociobiology Group (eds) Current problems in sociobiology. Cambridge University Press, Cambridge, pp 223–247

Clutton-Brock TH, Albon SD, Guinness FE (1985) Parental investment and sex differences in juvenille mortality in birds and mammals. Nature 313:131–133

Drickamer LC (1974) A ten year summary of reproductive data for free-ranging *Macaca mulatta*. Folia Primatol 21:61–80

Drickamer LC, Vessey SH (1973) Group-changing in free-ranging rhesus monkeys. Primates 14:359–368

Hrdy S (1987) Sex-biased parental investment among primates and other mammals: a critical evaluation of the Trivers-Willard hypothesis. In: Gelles R and Lancaster J (eds) Child abuse and neglect: biosocial dimensions. Aldine, New York, pp 97–147

Lindburg DG (1969) Rhesus monkeys: mating season mobility of adult males. Science 166:1176–1178

Meikle DB, Tilford BL, Vessey SH (1984) Dominance rank, secondary sex ratio and reproduction of offspring in polygynous primates. Am Nat 124:173–188

Sade DS (1967) Determinants of dominance in a group of free-ranging rhesus monkeys. In: Altmann S (ed) Social communication among primates. University of Chicago Press, Chicago, pp 99–114

Sade DS, Cushing K, Cushing P, Dunaif J, Figueroa A, Kaplan JR, Laver C, Rhodes D, Schneider J (1977) Population dynamics in relation to social structure on Cayo Santiago. Yearb Phys Anthropol 20:253–262

Siegel S (1956) Nonparametric statistics for the behavioral sciences. McGraw Hill, New York

Silk JB, Clark-Wheatley CB, Rodman PS, Samuels A (1981) Differential reproductive success and facultative adjustment of sex ratios among captive female bonnet macaques. Anim Behav 29:1106–1120

Silk JB (1983) Local resource competition and facultative adjustment of sex ratios in relation to competitive ability. Am Nat 121:56–66

Trivers RL, Willard DE (1973) Natural selection of parental ability to vary the sex ratio of offspring. Science 179:90–92

Vandenbergh JG (1967) The development of social structure in free-ranging rhesus monkeys. Behaviour 29:179–194

Vessey SH, Meikle DB (1984) Free-living rhesus monkeys: adult male interactions with infants and juveniles. In: Taub D (ed) Primate Paternalism. Van Nostrand Reinhold, North Scituate, MA, pp 113–126

Wilson ME (1981) Social dominance and female reproductive behavior in rhesus monkeys (*Macaca mulatta*). Anim Behav 29:472–482