

## SHORT COMMUNICATION

## Sons of Low-ranking Female Rhesus Macaques Can Attain High Dominance Rank in Their Natal Groups

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**ABSTRACT.** Five adult and subadult sons of middle- and low-ranking female rhesus macaques (*Macaca mulatta*) were observed to hold high dominance rank in their natal groups during a 12-month study at Cayo Santiago, Puerto Rico. Three of these males also experienced high mating success during at least one mating season. These findings contrast with all previously published accounts of rank acquisition by natal male rhesus macaques in provisioned colonies, and they present a challenge to the hypothesis that natal transfer functions to increase male access to fertile females.

**Key Words:** *Macaca mulatta*; Dominance; Dispersal; Cayo Santiago.

## INTRODUCTION

Dominance rank acquisition in gregarious nonhuman primates depends at least as much on social factors, such as the availability of powerful coalition partners, as on relative size and strength (WALTERS & SEYFARTH, 1987). A well-documented example of this generalization is the effect of maternal dominance rank on rank acquisition in male rhesus macaques (*Macaca mulatta*) that remain in their natal group as adults. Only sons of high-ranking females have been observed to acquire high rank themselves (KOFORD, 1963; KAUFMANN, 1967; TILFORD, 1982; CHAPPAIS, 1983). In this paper, I use new data to re-examine the relationship between maternal rank and natal male rank in rhesus macaques.

## METHODS

Three additional observers and I collected data on female mate choice in two social groups (groups T and Q) of free-ranging provisioned rhesus macaques at Cayo Santiago, Puerto Rico, during 12 months between May 1988 and August 1989. Complete genealogical and demographic records have been kept on this population since 1956 (SADE et al., 1985; RAWLINS & KESSLER, 1986). All individuals could be assigned to a matriline, which is defined as a group of monkeys descended from the same founding ancestress among the females alive in 1956.

Although I conducted focal animal follows on females only, my data collection protocol included ad lib. recording of dominance interactions (supplants, fear grimaces, chases, and contact aggression) among adults and adolescents of both sexes. I ascertained dominance relationships by arranging individuals in matrices showing winners of

dominance interactions along one axis and losers along the other. As a measure of mating success, I calculated, for each adult (> 4.5 yrs) and subadult (4.5 yrs) male, a mean hourly rate (averaged over estrous female focal subjects) of ejaculations with peri-ovulatory (i.e. potentially fertile) females. For further details, see MANSON (1991, 1992) and MANSON and PERRY (1993).

## RESULTS AND DISCUSSION

Like previous investigators of rhesus macaques (e.g. KAUFMANN, 1967; SADE, 1967; VESSEY & MEIKLE, 1987), I found that (1) both sexes form linear dominance hierarchies; (2) adult female dominance rank is genealogically determined, such that each female holds a rank below her mother and above her next oldest sister; (3) natal males do not acquire a stable dominance rank until age 5.5 yrs; and (4) immigrant male dominance rank is strongly positively correlated with group tenure (MANSON, 1991, 1992; MANSON & PERRY, 1993).

Dominance relationships of some dyads of low-ranking males could not be determined because we observed no interactions between the two animals. For analytical purposes, I assigned males of uncertain rank (8–38.7% of males) a rank that was the median rank of all the males of uncertain rank in their social group. Ties in mating success rank were handled similarly.

Table 1 shows the age, dominance rank, mother's dominance rank, and mating success rank (relative to all adult and subadult males in the same social group) of all natal males aged 5.5+ yrs that were resident in one of the study groups during at least one mating season of the study. In both study groups in both mating seasons, at least two sons of middle- or low-ranking females (i.e. females not in the highest ranking matriline) held dominance ranks in the top quarter of the male dominance hierarchy. In group Q in both mating seasons of the study, and in group T in one mating season, at least one son of a middle- or low-ranking female attained a mating success rank in the top 10%. Natal males'

**Table 1.** Age, dominance rank, mother's dominance rank, and mating success rank of natal males.

ID	Group	Mating season							
		1988				1989			
		Age <sup>1)</sup>	Rank <sup>2)</sup> (HS) <sup>3)</sup>	Mother's rank <sup>2)</sup> (HS) <sup>3)</sup>	Mating rank <sup>2)</sup> (HS) <sup>3)</sup>	Age <sup>1)</sup>	Rank <sup>2)</sup> (HS) <sup>3)</sup>	Mother's rank <sup>2)</sup> (HS) <sup>3)</sup>	Mating rank <sup>2)</sup> (HS) <sup>3)</sup>
D10	Q	7.5	.93 (31)	.78* (30)	.80 (31)	8.5	.92 (27)	.78* (37)	.81 (27)
D91	Q	6.5	.90 (31)	.78* (30)	1.00 (31)	7.5	.89 (27)	.78* (37)	.85 (27)
D71	Q	7.5	.87 (31)	.24 (30)	.89 (31)	8.5	.85 (27)	.25 (37)	.91 (27)
E05	Q	6.5	.84 (31)	.00 (30)	.97 (31)	7.5	.81 (27)	.03 (37)	.96 (27)
I32	Q	4.5	—	—	—	5.5	.77 (27)	1.00* (37)	.91 (27)
H53	Q	4.5	—	—	—	5.5	.17 (27)	.25 (37)	.17 (27)
G06	T	5.5	.97 (37)	.95# (21)	.97 (37)	6.5	.98 (42)	.95# (27)	.98 (42)
G26	T	5.5	.83 (37)	.65 (21)	.42 (37)	6.5	.88 (42)	.68 (27)	.46 (42)
G22	T	5.5	.80 (37)	.35 (21)	.42 (37)	6.5	.38 (42)	.34 (27)	.46 (42)
G41	T	5.5	transfer <sup>4)</sup>	.70 (21)	—	6.5	.17 (42)	.72 (27)	.46 (42)
H51	T	4.5	—	—	—	5.5	.86 (42)	.57 (27)	.95 (42)
H47	T	4.5	—	—	—	5.5	.17 (42)	.68 (27)	.46 (42)
H59	T	4.5	—	—	—	5.5	.17 (42)	.23 (27)	.46 (42)

1) In years; 2) proportion of same-sexed individuals (age 4.5+) outranked within the social group; 3) hierarchy size (number of individuals); 4) transferred out of group T in 1988 and returned to group T in 1989. \* In highest ranking of three matriline; # in higher ranking of two matriline.

copulatory partners tended not to be matrilineally related to them (MANSON & PERRY, 1993).

Because I did not conduct focal follows of males, I cannot easily test among alternative hypotheses regarding determinants of rank acquisition in natal males. Maternal rank is clearly one determinant, since sons of high-ranking females tended to outrank same-aged sons of low-ranking females. Continuity in group residence is apparently necessary for rank maintenance: males *G22* and *G41* transferred out of group T and returned to hold very low ranks. Sons of low-ranking females may have increased their chances of rising in rank by (1) forming alliances with other males, whether kin or non-kin, and/or (2) forming affiliative relationships with females of higher-ranking matrilines. CHAPAIS (1986) describes non-sexual male-female affiliative relationships between non-kin in this population.

It has been hypothesized that, in female-philopatric primate species, most males transfer from their natal group upon reaching sexual maturity because the costs of transfer are outweighed by the benefits of increased access to fertile females (PUSEY & PACKER, 1987). This situation is claimed to result from (1) female mate choice for novel over familiar males (e.g. PACKER, 1979), and, in macaques, (2) the inability of males (other than sons of very high-ranking females) to acquire high dominance rank in their natal group (BERARD, 1990). MANSON and PERRY (1993) have shown that (1) female rhesus macaques distinguish between their matrilineal relatives and unrelated natal males in choosing mates, and (2) young natal males experience high copulatory success with fertile females. Here I have shown that even sons of low-ranking females can attain high dominance rank in their natal groups, although they apparently cannot outrank natal sons of higher-ranking females. Transfer might lead eventually to even higher rank via "seniority" (e.g. VESSEY & MEIKLE, 1987). But this benefit must be discounted by the intervening time interval, whereas high rank and high mating success are attainable in the natal group within the first few years of adulthood.

My results must be qualified by noting that (1) I did not determine whether natal males can experience high rank and mating success for more than a few years (Table 1 shows that no natal males over 8.5 years remained in either study group), and (2) demographic conditions peculiar to Cayo Santiago (a small number of very large groups) may be responsible for my findings (e.g. natal males in small wild groups have access to fewer unrelated females that would choose them as mates).

Because transferring male rhesus macaques usually enter new social groups at the bottom of the dominance hierarchy and advance slowly (VESSEY & MEIKLE, 1987), the question of why most males leave their natal group remains a major challenge for investigators of this species.

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