

## Male aggression: a cost of female mate choice in Cayo Santiago rhesus macaques

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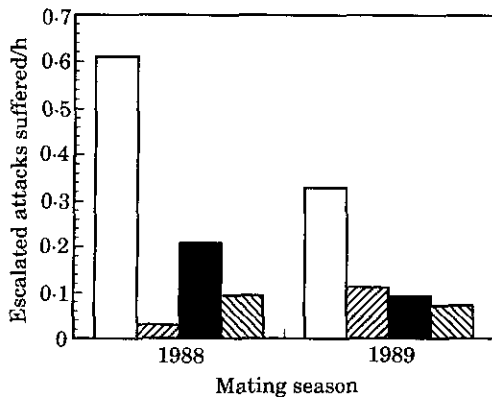
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Aggression from courting males is considered a potential cost of female mate choice, and hence a likely selective force on female mating behaviour (Parker 1979; Smuts & Smuts 1992). In species with male dominance hierarchies, females may respond to the threat of courtship aggression by choosing dominant, protective males that can protect them from harassment by subordinate males (e.g. Clutton-Brock et al. 1988). If, however, females incur apparent costs by failing to choose dominant males consistently, it may be hypothesized that an overcompensating benefit (e.g. parental care, genetic quality) accrues to them as a consequence of their choices (e.g. Pomiankowski 1987). In this report, building on previous findings that oestrous female rhesus macaques, *Macaca mulatta*, maintain proximity preferentially to lower-ranking males (Manson 1992), I show that females suffer higher rates of male attack while in proximity to low-ranking males than while in proximity to high-ranking males.

Four observers 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, on 211 days during the 1988 and 1989 mating seasons (for more information about the study site, see Rawlins & Kessler 1986). During 30-min focal follows on randomly chosen oestrous females, we recorded, among other data: (1) all approaches and leaves involving focal females and sexually mature males, (2) all completed copulations, (3) all escalated attacks (chases and bites) by males against focal females, and (4) the identity of the female's nearest adult male neighbour (hereafter, 'nearest neighbour') at 3-min intervals and at the moment of each escalated attack. Some eligible females (12 of 51, 23.5%, in 1988; 35 of 63, 55.5%, in 1989) were not selected as focal subjects; their average

dominance rank did not differ significantly from that of focal subjects. We collected 657 h of usable data on 48 different oestrous females. In comparisons among heterosexual dyads, female responsibility for proximity maintenance was significantly positively correlated with copulation rate during the female's periovulatory period (Manson 1992). Thus, female proximity maintenance represented mate choice, as defined by Halliday (1983). Females maintained proximity preferentially to lower-ranking males (Manson 1992). This preference probably reflected differences in the tactics necessary to achieve copulations with males of different dominance ranks, rather than preference for lower-ranking mates per se (Manson 1992).

Male rhesus macaques frequently chase, and occasionally bite, oestrous females that are accompanying lower-ranking males (Chapais 1983; Manson 1992). In one documented case in a wild population, a male fatally wounded an oestrous female in this context (Lindburg 1971). Of 200 escalated attacks observed during my study, 18 (9%) were either carried out by a male that did not belong to the female's social group, or occurred when the female's nearest neighbour was an adult male that did not belong to her social group. In 63 cases (31.5%), the female was attacked by her nearest neighbour. Of the remaining 119 (59.5%) cases, the attacker was higher-ranking than the nearest neighbour in 112 cases (94%). We never observed a nearest neighbour defend a female against attack by a higher-ranking male. To determine the effects of the nearest neighbour's dominance rank on the likelihood of attack against oestrous females, I divided males into two equal-sized groups, high- and low-ranking. I then divided the number of escalated attacks that each female suffered when a male of each rank class was her nearest neighbour by the number of focal hours during which a male



**Figure 1.** Mean hourly rate of male escalated attack on oestrous females in relation to dominance rank class of the female's nearest adult male neighbour, and identity of the attacker: low-ranking neighbour, attack by intruder (□); low-ranking neighbour, attack by neighbour (▨); high-ranking neighbour, attack by intruder (■); high-ranking neighbour, attack by neighbour (▩).

of that rank class was her nearest neighbour, yielding the hourly rates of attack suffered while males of the two rank classes were her nearest neighbours. Attacks while the female's nearest neighbour was not a member of her social group (7.5% of attacks) were excluded from this analysis. I divided attacks into (1) those in which a second male (an intruder) attacked and (2) those in which the nearest neighbour himself attacked. In both mating seasons, females suffered higher rates of attack by intruders while with low-ranking than with high-ranking males (Fig. 1; Wilcoxon test, excluding cases in which both values were zero: 1988:  $N=27$  females,  $T=106$ ,  $P=0.047$ ; 1989:  $N=16$ ,  $T=24$ ,  $P=0.023$ ). Attack rates by the nearest neighbour did not differ as a function of his rank class (1988:  $N=12$ ,  $T=21$ ,  $P=0.159$ ; 1989:  $N=12$ ,  $T=29$ ,  $P=0.434$ ). Attack rates by intruders were higher than attack rates by nearest neighbours for both rank classes of nearest neighbours in 1988 and for low-ranking nearest neighbours in 1989 (1988 high-ranking:  $N=20$ ,  $T=37$ ,  $P=0.011$ ; 1988 low-ranking:  $N=16$ ,  $T=0$ ,  $P=0.0005$ ; 1989 high-ranking:  $N=11$ ,  $T=20.5$ ,  $P=0.266$ ; 1989 low-ranking:  $N=10$ ,  $T=6.5$ ,  $P=0.0323$ ).

Because focal subjects (1) maintained proximity preferentially to lower-ranking males and (2) tended to restore proximity to nearest neighbours following attacks by intruders (Manson 1992), it is unlikely that male attacks are ritualized

displays enabling females to evaluate male quality. Rather, females choose mates independently of male dominance rank, even though they could minimize costs by consistently choosing (i.e. maintaining proximity to) high-ranking males. Provisioning, absence of predators, and inoculation against tetanus (Kessler et al. 1988) at Cayo Santiago presumably ameliorate the effects of wounding on fitness. The unusually high adult sex ratios of Cayo Santiago rhesus macaques may elevate the risk of male attacks against oestrous females (Manson 1992). Available data do not permit measurement of the costs to females of male attacks in the rhesus macaque 'environment of evolutionary adaptedness' (Bowlby 1969). If male attacks are costly to females, overcompensating benefits should accrue to females as a result of their mate choices. These benefits do not include male parental investment, as males do not care for infants and show no tendency to associate with past mates during the following birth season (Hill 1990). Hypotheses yet to be tested include: (1) females choose mates on the basis of genetic quality, and male genetic quality is independent of dominance rank; and (2) females benefit (e.g. by increasing the genetic variability among their offspring) by choosing sexually novel males (Huffman 1991) that are likely to be of low rank because dominance rank is positively correlated with group tenure (Vessey & Meikle 1987).

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