Supportive and tolerant relationships among male Tibetan macaques at Huangshan, China

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Summary

Tibetan macaque males at Huangshan (Macaca thibetana huangshanensis) display highly skewed mating success and highly asymmetric patterns of aggression, but also high levels of tolerance. We examined affiliation, tolerance and agonistic support to test the hypothesis that increased tolerance in otherwise despotic males may occur when high-ranking males require support from other males to prevent (1) potentially destabilizing revolutionary coalitions against them, or (2) young adult males from usurping the alpha position. Several predictions of the first hypothesis were supported: Support was unrelated to kinship or affiliation and was generally conservative, serving to reinforce the current hierarchy. Nevertheless, revolutionary coalitions posed a threat, particularly to alpha males. High-ranking males displayed tolerance in the form of co-feeding toward lower ranking males that supported them, and alpha males showed the most cooperation with the males that targeted them in revolutionary coalitions. Predictions of the second hypothesis were not consistently supported; male coalitions targeted young potential usurpers of the alpha position during only one of two periods of hierarchical stability. We suggest that high ranking males discourage revolutionary alliances by using two strategies. They primarily rely on conservative alliances, but also offer tolerance in cases in which conservative coalitions are less effective.

Keywords: Macaca thibetana, male cooperation, agonistic support, reciprocity, male tolerance.

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Introduction

From a socio-ecological point of view, affiliation, tolerance and cooperation should be less common among male than female socially-living primates (van Hooff & van Schaik, 1992, 1994; van Schaik, 1996). This prediction follows from the premise that individual male reproductive success depends primarily on fertilizing females, who represent limited and unshareable resources, whereas individual female reproductive success depends primarily on acquiring adequate nutrition and protection (potentially shareable resources). Thus male-male competition over access to fertile females is expected to constrain opportunities for affiliation, tolerance and cooperation.

Among non-human primates, males may compete by monopolizing either single females, resulting in monogamy, or groups of females, resulting in one male, multi-female groups (van Hooff & van Schaik, 1992; van Schaik, 1996). If neither is possible, or if other factors, such as a high need for vigilance, favor the presence of multiple males, males may co-exist in multi-male, multi-female groups (e.g., Srivastava & Dunbar, 1996; van Hooff, 2000) and attempt to gain disproportionate shares of paternity through various forms of within-group contest or scramble competition (van Hooff & van Schaik, 1992; van Schaik, 1996; Kappeler, 2000). The potential for within-group competition among males is expected to be lower in groups with relatively small numbers of competing males per female than in groups with nearly even sex ratios. Thus at first glance, one might expect to find more male-male affiliation, tolerance and cooperation in groups with few males per female than in groups with nearly even sex ratios.

Contrary to this expectation, several researchers have noted that among macaques, species that typically display male affiliation and tolerance tend to be those with nearly even sex ratios, whereas those with lower male:female ratios typically display little male affiliation or tolerance (Hill, 1994 and references therein; Ogawa, 1995a, b; Menard & Vallet, 1996; Preuschoft et al., 1998; Cooper & Bernstein, 2002). To account for this apparent discrepancy, Ogawa (1995a) hypothesized that nearly even adult sex ratios, such as those in Tibetan macaques at Huangshan (Macaca thibetana huangshanensis) (Wada & Xiong, 1996), lead to both high levels of male-male competition and enhanced mechanisms to cope with potential and actual conflict.

Preuschoft & Paul (2000) predicted that nearly even sex ratios and the high levels of male-male competition they engender can lead to tolerance