



Paternity analysis of alternative male reproductive routes among the langurs (*Semnopithecus entellus*) of Ramnagar

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Because primate males usually invest very little in offspring, male reproductive success will mainly be determined by access to fertile females with differences in access leading to differential male reproductive success. To determine the outcome of alternative male reproductive routes, we investigated a wild population of Hanuman langurs at Ramnagar, South Nepal, where groups were either one-male or multimale. Paternity was established by DNA analysis from faeces for 42 infants in five groups. In one-male groups all infants were sired by the only resident male in the group. In multimale groups the alpha male fathered significantly more infants (57%) than all other resident males. Nonresident males sired at least 21% of all infants born into multimale groups. Because of the lower mean number of infants sired by alpha males during their whole tenure as alpha compared with males in one-male groups (2.3 versus 6.8) and the higher maximum value (8.9 versus 6.0), the alpha male route is considered the riskier option. Based on demographic data we suggest that the considerable variance in short-term reproductive success might not translate to the same degree into differences in long-term reproductive success.

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Primates are characterized by a long period of parental investment, mostly performed by females. Therefore, different reproductive strategies are expected for primate males and females (Trivers 1972). While female reproductive success will mainly be limited by physical capabilities and hence food availability, male reproductive success will mainly be determined by access to fertile females. It is assumed that the distribution of females basically determines the distribution of males (e.g. Emlen & Oring 1977; Altmann 1990; Mitani et al. 1996).

To maximize his lifetime reproductive success, a primate male should try to reproductively monopolize as many females for as long as possible. Male–male competition for access to fertile females should then lead to differential male reproductive success (Darwin 1859; Andersson 1994). The best option for males would be to monopolize a whole group of females (i.e. a one-male group). Under conditions of reduced monopolizability of females, when multimale groups form, males should still

try to monopolize access to females. Despite a long-standing debate on the influence of dominance on male reproductive success in primates (e.g. Robinson 1982; Fedigan 1983; Bercovitch 1991), high dominance rank in multimale groups is often expected to lead to high reproductive success (priority of access: Altmann 1962; Suarez & Ackerman 1971).

During the past few years the application of DNA typing techniques to paternity determination enabled direct testing of the relationship between dominance rank and reproductive success in male primates, but the results are equivocal. In a number of studies a positive relationship was found (e.g. *Cercocebus torquatus atys*: Gust et al. 1998; *Macaca arctoides*: Bauers & Hearn 1994; *M. fascicularis*: de Ruiter et al. 1992; *M. mulatta*: Bercovitch & Nürnberg 1997; *Mandrillus sphinx*: Dixon et al. 1993; *Papio cynocephalus*: Altmann et al. 1996). Other studies, however, yielded no relationship or even a negative relationship (e.g. *Lemur catta*: Pereira & Weiss 1991; *Macaca fascicularis*: Shively & Smith 1985; *M. mulatta*: Berard et al. 1993; *M. sylvanus*: Witt et al. 1981).

Lack of a positive relationship between dominance rank and reproductive success in multimale groups was attributed to several factors that might act on male

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