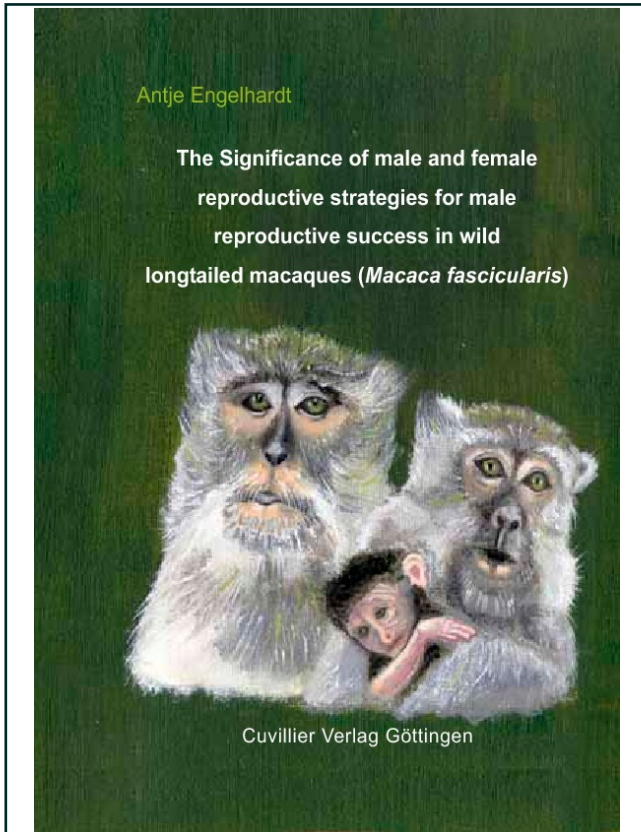




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The significance of male and female reproductive strategies for male reproductive success in wild longtailed macaques (*Macaca fascicularis*)



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Reproductive strategies and the ‘struggle of the sexes’ in primate multimale groups: an introduction

Evolution and the ‘Struggle of the Sexes’

The theory of sexual selection is nowadays commonly invoked to explain primate behaviour and evolution, although details of the proximate mechanisms involved remain poorly understood. Darwin already noted that females are apt to be the choosy sex and males the competitive sex due to differences in offspring investment. Although Fisher’s (1930) ‘runaway model’ and Zahavi’s (1975) ‘handicap principle’ strongly supported the idea of sexual selection for female mate preference, primatologists have for a long time seen female primates as the ‘passive’ sex, and males as actively determining reproductive events. Just recently, the importance of female reproductive strategies has become increasingly recognized, but still, little is known about the adaptive value of female reproductive strategies and their interaction with male reproductive strategies (Chism & Rogers 1997; Janson 1984; Small 1989; Taub 1980; Vasey 1998; Small 1989; Sterck et al. 1997). Sexual selection acts differently on males and females as females, especially in mammals, allocate a great proportion of their lifetime to parental effort through pregnancy and lactation, which limits the number of offspring a female mammal can produce in her lifetime. Males, on the other hand, produce lots of small, ‘cheap’ microgametes, predisposing them to maximize the number of successful matings. Thus, while males should compete for access to fertile females, females should ensure a high reproductive rate and survival of their offspring and, therefore, should be choosy in with whome they mate (Darwin 1871; Trivers 1972). As a consequence, reproductive strategies of the genders may even counteract each other and lead to inter-sexual conflict over reproduction (e.g. Trivers 1972; Smuts & Smuts 1993; Clutton-Brock & Parker 1995; Gowaty 1996; Nunn & van Schaik 2000).

Male and Female Sexual Strategies in Multimale Primate Groups

According to sexual selection theory, contest competition among males for access to mating partners should lead to polygynous socio-sexual systems where sexual dimorphism in body weight and canine size clearly exists (Mitani et al. 1996; Plavcan & van Schaik 1997) and in which the strongest male gains exclusive access to fertile females (priority of access to fertile females model; Altmann 1962; see also Fedigan 1983). However, a lot of primate species are organized in multimale groups. In these groups, males form dominance hierarchies, which often seem to be the most important factor influencing a male's reproductive success (e.g. *Cercocebus torquatus atys*: Gust et al. 1998; *Macaca fascicularis*: de Ruiter et al. 1994; *Macaca sylvanus*: Paul & Kuester 1996; *Mandrillus sphinx*: Dixson et al. 1993; *Papio cynocephalus*: Altmann et al. 1996; *Presbytis entellus*: Launhardt et al. 2001). This, however, is not always true and in some primate species, significant numbers of offspring are fathered by nondominant or extra-group males (e.g. *Macaca fuscata*: Inoue et al. 1993; Soltis et al. 2001; *Macaca mulatta*: Berard et al. 1993, 1994; Widdig et al. 2004; *Papio cynocephalus*: Alberts et al. 2003). The proximate mechanisms underlying these variations in reproductive success of dominant males in multimale primate groups still remain largely unknown.

A factor that seems to affect monopolizability of females by dominant males is cycle synchrony, because a single male can hardly monopolize more than one female at a time (Paul 1997; Nunn 1999a). Furthermore, subordinate males may form coalitions in order to break up consortships between high-ranking males and fertile females (e.g. *Papio cynocephalus*: Packer 1977; Noë & Sluijter 1990; Bercovitch 1995) or extra-group males might try to sneak copulations without notice of other males (e.g. *Macaca fuscata*: Soltis et al. 2001). Female monopolizability may also depend on female cooperation. The significance of female cooperation for male reproductive success, however, is still under discussion (Bercovitch 1995).

Even when fertile females are not monopolized by dominant males, males in general may still coerce matings (reviewed in Smuts & Smuts 1993) and thus restrict female freedom to display their own mating preferences. On the other hand, females that are able to resist mating attempts gain freedom to exert their own reproductive strategies. Small (1989) has suggested that females should actively choose the male with the 'best genes' to father their offspring in order to improve the offspring's genetic strength ('direct female choice'). On the other hand, females may benefit from mating polyandrously (reviewed in Wolff & Macdonald 2004), thus avoiding inbreeding or genetic incompatibilities (e.g. Tregenza & Wedell 2002;

Newcomer et al. 1999; reviewed in Zeh & Zeh 2001) or receiving high quality fertile sperm through sperm competition (Dixson 1998), since competition between spermatozoa of rival males will occur when females mate with more than one male (Parker 1970). Females may benefit from sperm competition if sperm quality is positively related to offspring fitness (Parker 1992) or if sons inherit the competitive ability of sperm from their fathers (Harvey and Bennet 1985). The observation that primate males living in multimale groups have higher testis to body weight ratios compared to those living in one-male groups or in monogamous mating systems has been interpreted as a result of sperm competition (Harcourt et al. 1981).

Apart from genetic benefits, other motives could drive females to mate with many males, for example, the attempt to tighten males to the group, as the number of males present in a group can affect the predation rate (Van Schaik & Höstermann 1994; Stanford 1998), and superiority in intergroup encounters (*Cercopithecus aethiops*: Cheney & Seyfarth 1987; *Macaca fuscata*: Kawanaka 1973). Furthermore, in several primate species, males kill infants of females with which they have previously not mated before (*Alouatta spec.*: reviewed in Crockett 2003; *Papio cynocephalus*: reviewed in Palombit 2003; *Trachypithecus entellus*: reviewed in Borries & König 2000; *Macaca fuscata*: Soltis et al. 2000). Though the adaptive value of infanticidal behaviour has not yet been fully established (Niemitz 1997), there is increasing evidence that males benefit from killing dependant infants of which they are not the father by mating with the mother soon after the killing, because these females usually become receptive again more quickly than lactating females (Hrdy 1974; Borries et al. 1999; van Schaik et al. 2000). For the female, infanticide poses a great cost, as the time and energy she has already invested in her former offspring is lost. Consequently, polyandrous mating may be a counterstrategy against infanticide, because it leads to paternity confusion (Hausfater & Hrdy 1984). Another female counterstrategy is proposed by the bodyguard hypothesis, which suggests that females mate preferentially with strong males who in future protect the ensuing infant (Mesnick 1997). This might have been the origin of the so-called 'friendships' observed in savannah baboons (Smuts 1985, 1987).

Thus, it seems that females would benefit from both concentrating matings to a single, strong male and from mating polyandrously. A more recent hypothesis proposes a way in which females are able to bias paternity towards strong males and, at the same time, reduce the risk of infanticide by paternity confusion. The graded-signal hypothesis (Nunn 1999b) suggests that females display a graded signal which indicates the probability of ovulation, but not its precise timing. In this way, females could mate polyandrously with subordinate males when the signal is low, as is the probability to conceive, and on the other hand attract

dominant males when the signals have reached their maximum, i.e. when probability of conception is high. Since the probability of conception is low but not zero during the period in which subordinate males mate with females, all mating partners are potential fathers of the ensuing offspring and, thus, should avoid infanticide.

In contrast to the example given above, female mate choice is not always obvious: female participation in male-male aggressive interactions might be a form of female choice (indirect female choice; Smuts 1987), as it can influence group membership and, in doing so, can determine who will be available as mates. Furthermore, a variety of mechanisms might allow females to be choosy after copulation (female cryptic choice; reviewed in Reeder 2003): females may discard or destroy sperm of unfavoured males, hinder sperm transport to fertilization sites, choose among sperm that have reached the egg or abort zygotes.

Thus, male and female reproductive strategies can either occur on the precopulatory level (male contest competition, male coercion, sneaking copulations, female direct or indirect choice) or on the postcopulatory level (sperm competition, cryptic female choice). On which level individual male success to fertilize a female is determined and to what extent the different reproductive strategies are involved remains unclear so far. The crucial period within an ovarian cycle, in which the adaptive value of precopulatory behaviours as well as the potential for postcopulatory mechanisms is determined, is the fertile phase.

The Fertile Phase and its Potential Cues

Timing of copulations is suggested to be a more important factor for male reproductive success than the number of copulations with a certain female, as the period within an ovarian cycle, in which a copulation can lead to conception (fertile phase), is limited to a few days around the time of ovulation (Gomendio et al. 1998). Since matings outside the fertile phase do not lead to conception, the ability to recognize this period is clearly important for males and can significantly reduce male reproductive costs. On the other hand, female masking of the fertile phase, so that males do not know when to monopolize or coerce females, increases female freedom to pursue their own reproductive strategies (see above). Since female sexual activity is well extended over the fertile period (reviewed in van Schaik et al. 2000), for a long time it was unclear whether the fertile phase was concealed from primate males. Just recently, a study on Hanuman langurs carried out under natural conditions showed that timing of ovulation is concealed from males in this species (Heistermann et al. 2001) and that the dominant male lost over 80% of paternities to low-ranking males, because

he did not adjust mate guarding to the time around ovulation. However, time of ovulation seems not to be concealed from male anthropoid primates in general, since captive male macaques are most attracted by females around the time of ovulation (reviewed in Michael & Zumpe 1993; Zumpe & Michael 1996; see also Aujard et al. 1998). Whether these results can be applied to natural situations, however, is still unknown, because studies, which have tested the ability of male macaques to discern the fertile phase, are still missing for wild groups.

There are different mechanisms by which male primates could recognize a female's reproductive state. Given the fact that the fertile phase coincides with a period of elevated ovarian oestrogen levels, those female traits that closely correlate with oestrogens carry the potential to indicate the fertile phase in particular. Certain volatile aliphatic acids, for example, which have been identified in the vaginal discharge of many different primate species (reviewed in Hrdy & Whitten 1987), change in concentration according to changes in female oestrogen levels and enhance male interest, so that they have been interpreted as sex pheromones (Curtis et al. 1971; Michael & Keverne 1968, 1970; Michael et al. 1971, 1977; but see Goldfoot et al. 1978; Goldfoot 1981). Whether males make use of these cues under natural conditions, however, still needs to be investigated.

A possible visible sign of female reproductive status is the sexual swelling of skin, which occurs mainly in catarrhine primate species living in multimale groups (reviewed in Hrdy & Whitten 1987). Swelling size changes in accordance to female oestrogen and progesterone levels (e.g. Parkes & Zuckerman 1931; Gillman 1940; Carlisle et al. 1981; Ozasa & Gould 1982; Onouchi & Kato 1983), with male sexual motivation being highest when the skin is fully tumescent (Bielert & van der Walt 1982; Girolami & Bielert 1987; Bielert et al. 1989; Dixson 1998; Deschner et al. in press). Different hypotheses have been proposed to explain the specific function of sexual swellings (reviewed in Zinner et al. 2004), including those, which predict that the swelling size reliably indicates the fertile phase (reliable-indicator hypothesis, Hamilton 1984), but although in some primate species sexual swellings are a good approximation for the female periovulatory phase (e.g. *Macaca nigra*, *Papio cynocephalus*; for a review see Nunn 1999b), they do not always reliably indicate this period (see Nunn 1999b; see also Reichert et al. 2002; Deschner 2003). Another model, the graded-signal hypothesis (Nunn 1999b), proposes that graded swellings serve to enable females to mate polyandrously during periods with low probability of conception and to bias paternity towards dominant males by mating with these males during periods of high probability of conception (see above). To date, the specific functions of sexual swellings