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Determinants of male reproductive success in wild long-tailed macaques (*Macaca fascicularis*) – male monopolisation, female mate choice or post-copulatory mechanisms?

ANTJE ENGELHARDT[ab], MICHAEL HEISTERMANN[a], J. KEITH HODGES[a], PETER NÜRNBERG[c] AND CARSTEN NIEMITZ[b]

[a] Department of Reproductive Biology, German Primate Centre
[b] Human Biology and Anthropology, Free University of Berlin
[c] Institute of Medical Genetics, Charité, Humboldt-University Berlin; now Centre for Genomics, University of Cologne

Corresponding author:
Antje Engelhardt
Institute for Mind and Biology, University of Chicago,
940 E. 57th Street, Chicago, IL 60637, U.S.A.
Phone: +1-773-834-4658
Fax: +1-773-702-0320
antje@uchicago.edu

Abstract

One of the basic principles of sexual selection is that male reproductive success should be skewed towards strong males in species with anisogamous sex. Studies on primate multi-male groups, however, suggest that other factors than male fighting ability might also affect male reproductive success. The proximate mechanisms leading to paternity in multi-male primate groups still remain largely unknown since in most primate studies mating rather than reproductive success is measured. Furthermore, little research focuses on a female's fertile phase. The aim of this study was to investigate the relative importance of male monopolisation and female direct mate choice for paternity determination. We also investigated the extent to which paternity was decided post-copulatory, i.e. within the female reproductive tract. We used a combined approach of behavioural observations with faecal hormone and genetic analysis for assessment of female cycle stage and paternity, respectively. The study was carried out on a group of wild long-tailed macaques living around the Ketambe Research Station, Gunung Leuser National Park, Indonesia. Our results suggest that both male monopolisation and post-copulatory mechanisms are the main determinants of male reproductive success, whereas female direct mate choice and alternative male reproductive strategies appear to be of little importance in this respect. Female cooperation may, however, have facilitated male monopolisation. Since paternity was restricted to alpha and beta males even when females mated with several males during the fertile phase, it seems that not only male monopolisation, but also post-copulatory mechanisms may operate in favour of high-ranking males in long-tailed macaques, thus reinforcing the reproductive skew in this species.

Keywords: reproductive strategies, primates, paternity, post-copulatory mechanisms, *Macaca fascicularis*

INTRODUCTION

A fundamental question in primate sexual selection concerns the proximate mechanisms underlying male reproductive success in multi-male groups. According to sexual selection theory, males should compete for access to receptive females, the resource that limits male reproductive success the most (Trivers 1972). Contest among males for access to mates, in turn, should lead to social systems in which the strongest male is able to monopolise access to fertile females (priority of access to oestrus females model: Altmann 1962; see also Fedigan 1983). The finding that dominant males often sire the majority of offspring clearly shows that dominance plays an important role for male reproductive success in mammals (Ellis 1995), including primates (e.g. *Cercocebus torquatus atys*: Gust et al. 1998; *Macaca sylvanus*: Paul & Kuester 1996; *Mandrillus sphinx*: Dixson et. al. 1993; *Papio cynocephalus*: Altmann et al. 1996). Complete monopolisation of females is, however, difficult to achieve. In some primate species, subordinate and extra-group males have a significant share in paternity (e.g. *Macaca fuscata*: Inoue et al. 1993; Soltis et al. 2001; *Macaca mulatta*: Berard et al. 1993, 1994; Widdig et al. 2004), which indicates that other mechanisms operate as well in determining paternity. Thus, the importance of female and alternative male reproductive strategies as well as the interactive aspects of these has become increasingly recognised in recent years (e.g. Taub 1980; Janson 1984; Small 1989; Manson 1994; Bercovitch 1995; Chism & Rogers 1997; Sterck et al. 1997; Soltis et al. 2000, 2001, 2004).

Successful monopolisation of access to fertile females depends on several factors (reviewed in Soltis 2004). One of these factors is synchrony of female ovarian cycles, because males are hardly able to successfully monopolise more than one female at a time (Paul 1997, Nunn 1999a). Fighting ability as well as coalition forming of subordinate males are also important determinants of male mating and mate guarding success, as has been shown for savannah baboons (*Papio cynocephalus*; Packer 1977; Bercovitch 1986; Noë & Sluijter 1990; Alberts et al. 2003). A third variable that may influence monopolisation of females is the degree to which females resist or cooperate with males (Bercovitch 1995) and it seems that in at least some primate species, females are able to resist mating attempts (e.g. *Macaca mulatta*, Manson 1992; see also Soltis 2004).

Females should pursue reproductive strategies for their own best fitness increase. These strategies could also be opposing to male reproductive interests leading to inter-sexual conflict over control of reproduction (e.g. Trivers 1972; Smuts & Smuts 1993; Clutton-Brock & Parker 1995; Gowaty 1996; Nunn & van Schaik 2000). Whether females are able to exert their own reproductive strategies, however, depends on the ability and degree of male coercion. Mate guarding by dominant males may be one of the strongest forms of male coercion if it is not based on female cooperation.

Whereas probability of paternity is affected on the pre-copulatory level (Paul 2002) (i.e. the level on which a behaviour can in- or decreases the probability of mating between two individuals) by male monopolisation and female mate choice, it will be affected on the post-copulatory level whenever mating is not concentrated on a single male during the fertile phase. As soon as several males mate with the same female during her fertile phase, sperm of the different males will compete for fertilisation and paternity will be determined within the female reproductive tract. The number and viability of sperm a male brings into competition has, in this respect, been suggested to markedly affect his chances of siring offspring (reviewed in Birkhead & Møller 1998; see also Birkhead 2000). It may also be that the female controls which male will fertilise her oocyte by, for example, discarding or destroying sperm from unfavoured males (cryptic female choice; reviewed in Eberhard 1996; Reeder 2003). It remains largely unknown to what extent post-copulatory selection of sperm from a particular male plays a role for male reproductive success in multi-male primate groups, although the potential for it seems to be apparent in the majority of primate species (Birkhead & Kappeler 2004).

Which of the pursued reproductive strategies eventually comes into effect leading to paternity depends on the events occurring during the female's fertile phase, i.e. the brief period within a female ovarian cycle when copulation can lead to conception. Since the objective assessment of female reproductive status was for a long time impossible in the wild, conclusions about primate reproductive strategies were mainly based on observations conducted over almost the whole female cycle. If studies were focused on the fertile phase, assessment of this period had to rely on secondary markers like sexual swellings that have only limited value (Nunn 1999b, Reichert 2002, Deschner 2003, Engelhardt et al. 2005). Recent studies, however, have shown that male and female reproductive behaviour can vary significantly according to the stage of the female cycle (Deschner et al. 2004; Stumpf & Boesch 2005). In this respect, concealment of the fertile phase has been interpreted as a female strategy to hamper mate guarding in order to achieve more freedom for own reproductive decisions (van Schaik et al. 2000; Heistermann et al. 2001). If the probability of ovulation is only gradually but not precisely signalled (graded-signal hypothesis; Nunn 1999b), females might be able to mate polyandrously with subordinate males during times with low (but not zero) probability of conception and to attract dominant males during times of higher probability. The ability to recognise the female fertile phase, on the contrary, can significantly affect male reproductive success. Since monopolisation of females is costly (Alberts et al. 1996), males benefit from discerning the fertile phase of a cycle by being able to restrict mating efforts and mate guarding to this period. Recognition of the fertile phase seems to occur at least to some degree in some primate species (*Macaca fascicularis*; Engelhardt et al. 2004; but see *Trachypithecus entellus*: Heistermann et al. 2001).

In long-tailed macaques, dominant males appear to father the majority of offspring (de Ruiter et al. 1994), the proximate mechanisms leading to the observed reproductive skew in favour of dominant males are, however, still unclear. The aim of our study was therefore to explore the determinants of male reproductive success in this species by investigating (1) the degree of male monopolisation, (2) female mating preferences and freedom for mate choice, and (3) the degree to which paternity is decided post-copulatory in a group of wild long-tailed macaques living in the Gunung Leuser National Park, North Sumatra, Indonesia. For this, we have combined detailed behavioural observations with non-invasive faecal progestogen and oestrogen measurements for assessing the female fertile phase and faecal microsatellite analysis for genetic paternity determination. This integrative approach allows us to evaluate the proximate mechanisms determining male reproductive success in primate multi-male groups under completely natural conditions.

METHODS

Animals and Study Site

The study was carried out at the Ketambe Research Station (3º41'N, 97º39'E), Gunung Leuser National Park, North Sumatra, Indonesia. The research area consists of primary lowland rainforest and has been described by Rijksen (1978) and van Schaik & Mirmanto (1985). Behavioural observations and faecal sample collection occurred from February 14 until December 16, 2000.

Tab. 1

The long-tailed macaques of the study area have been studied since 1979 and were well habituated to observers. The study focused on the group "House Atas" (HA). This group was one of three daughter groups ("House Atas", "House Bawah", HB, and "House Dapur", HD) of the former House group (B. Putragayo, pers. comment). At the beginning of the study, group HA consisted of eight adult females, five adult males and several subadults/juveniles and two infants. The home range of group HA overlapped with that of groups HB and HD and further with that of a third group, the Ketambe Bawah group (KB). Males from all adjacent groups and, in addition, those from a fifth nearby group (group "Antara") entered the home range of group HA from time to time and engaged in sexual interactions with females. The alpha male of group HB (alpha male HB) joined the group HA almost daily from beginning of March 2000 until mid-April 2000 (Fig. 2), but returned every night to sleep with his own group. All group members of the study group HA and all males that moved within the home range of HA, were individually known.

Hormone Analysis and Definition of the Fertile Phase

Faecal hormone extraction and analysis conducted for assessment of female cycle stage and timing of the fertile phase has already been described (details in Engelhardt et al. 2004). Briefly, 2–3 g faeces were collected from each adult female (Table 1) on four to seven days per week and stored in 15 ml absolute ethanol at 4°C until hormone analysis. Extracts were measured for concentrations of immunoreactive oestrogen (total oestrogens, iEtotal) and progestogen (pregnanediol-3-glucuronide, iPdG) metabolites. Both measurements have been shown to provide reliable information on female ovarian function and timing of ovulation in long-tailed macaques (Shideler et al. 1993; Engelhardt et al. 2004).

As described in Engelhardt et al. (2005), for each cycle, a defined rise in iPdG-level above a threshold value (two standard deviations above the preceding baseline level) was used to determine the presumed time of ovulation and to define the fertile phase (Fig. 1). We determined for each ovarian cycle a two-day period in which ovulation was most likely (ovulation window). This period comprised the days –2 and –3 relative to the faecal iPdG-rise (day 0). Given that mating in long-tailed macaques can be fertile when occurring up to two days before and on the day of ovulation (Behboodi et al. 1991), we defined the fertile phase to be the period comprising the two days of the ovulation window plus the two preceding days. In the following, non-conception cycles are numbered by occurrence and asterisks indicate conception cycles.

Fig. 1

Two cycles differed from the other cycles in that in one (KA2) ovulation did not occur (as indicated by lack of iPdG rise; in the cycle prior to and after this cycle the female did ovulate, Table 1), although female oestrogen levels were elevated and followed a normal pattern. In the other (SA1), oestrogen levels were elevated more than a week before the iPdG rise. In both cycles, however, female sexual activity and male interest in the female was increased during the period of elevated female oestrogen levels, as it was in normal ovulatory cycles. Since our earlier study showed that both female sexual activity and female attractivity to males are related to female oestrogen levels (Engelhardt et al. 2005) and since the pattern of male and female behaviour was comparable to that during the fertile phases of ovulatory cycles, we included data from the four days surrounding the day of maximum female oestrogen values into our behavioural analyses. The four days included started on day –2 relative to the day of maximum oestrogen value (day 0), which was on average the third day of the fertile phase during the regular ovulatory cycles.

Genetic Paternity Analysis

Faecal samples for paternity analysis were collected from all infants that were born subsequent to the observed conception cycles $(N = 6)$ and from their mothers. Furthermore, faecal samples from all 24 males that were observed moving within the home range of group HA were collected, irrespective of whether the males had been observed to interact with females or not. From fresh faeces, 2–3 g were stored in absolute ethanol at 4°C until extraction. Primers (D1S548, D2S367, D3S1768, D5S502, D6S266, D6S501, D8S271, D8S601, D14S255, D20S476, MFGT5), DNA extraction and PCR procedures are described by Engelhardt (2004).

We used the multiple-tube approach (Taberlet et al. 1996, 1999) for individual genotyping in order to overcome false genotyping. In this respect, if possible, we genotyped three different samples for each individual. If less than three faecal samples were available, we used at least three different DNA extracts from these samples. To be taken as true alleles, alleles of a specific locus had to be confirmed twice each in three independent PCRs. When a third allele emerged, PCR was repeated until the two most frequent alleles were confirmed at least four times each in independent PCR products from at least two different extracts. These alleles were then seen as the ‘true’ alleles (provided the third allele did not emerge a second time). In the rare cases that it was not possible to clearly determine two alleles for a certain locus, the locus was either omitted for the individual or all appearing alleles were taken as potential alleles of this individual. Homozygosity was confirmed if a single allele occurred in six independent PCRs or if a second allele occurred only once in eleven independent PCRs.

We compared the mother and offspring genotypes to deduce which infant allele was inherited from the father. If the mother and infant had the same two alleles or if we were not able to genotype a mother at a certain locus, both infant alleles were considered as potential paternal alleles. Males who did not match with the deduced paternal alleles at anyone’s locus were excluded from paternity. A male was considered the likely father, if (1) all other males were excluded from paternity, and (2) he was compatible with the paternal alleles in all genotyped loci (at least six). In only one case, no male matched with the deduced paternal alleles in all genotyped loci. In this case, the only male that had only one mismatch with the paternal alleles was assumed to be the likely father. We furthermore calculated parentage likelihood using the program CERVUS 2.0 (Tristan Marshall, Edinburgh, UK; Marshall et al. 1998) including only those alleles that matched our definition for 'true alleles'. All deduced paternities had a likelihood of ≥ 98%.

Behavioural Observations

Behavioural observations were conducted by A.E. supported by four experienced Indonesian field-assistants (Arwin, Matplin, Rahimin, Samsu) and three students from the Universities UNSYAH (Dewi, Surya) and STIKK (Azhar), Darussalam Bandah Aceh, Indonesia. Group HA was followed from dawn until dusk (mean observation time: 11.1 h) every day by two to three observers at the same time. During this time, sexual interactions occurring between an adult group member and any other individual were recorded in detail using the all occurrence sampling method (Altmann, 1974). For this, we noted the identity of the interacting partners and the occurrence or absence of the following behaviours: Female approaches male, male approaches female, female presents anogenital region to a male ("Präsentieren", Angst, 1974), female refuses sexual interaction (by moving away), male inspects female genitalia ("Inspizieren", Angst, 1974), male mounts, intromission, ejaculation pause. Furthermore all agonistic interactions (threatening, chasing, biting, grabbing and pulling a fleeing female to force copulation) between the sexual partners or with a third party during sexual interactions were noted on occurrence. Threatening, chasing and biting was collectively called harassment. In addition to agonistic interactions between group members, all agonistic interactions of males of the adjacent groups were recorded ad libitum (Altmann 1974).

Dominance rank within males and females was determined by the display of the 'bared-teeth-face', a unidirectional submissive display (van Hooff 1967), and with a sociometric matrix (Altmann 1974) in which the direction of aggression was entered. It was not possible to deduce the complete dominance hierarchies between males from all groups, but for each group the alpha and the beta male could be determined. The rank relation between the dominant male of group

HA and the dominant male of group HB, who temporarily joined group HA (see above), was undecided.

All adult females of group HA were observed as focal animals (Altmann 1974) every day for about two hours on row (mean: 2.1 h/day, range: 1.4 – 2.6 h/day), often two to three females simultaneously. During focal animal sampling, consortships were recorded with the continuous sampling method (Martin & Bateson 1993). Consortships were defined as taking place when an adult male and a sexually active adult female maintained in proximity within 10 m (when with the group) or within 20 m (when away from the group) for at least ten consecutive minutes and when coordinated movements occurred. Usually, consort partners engaged in sexual interactions with each other, but sometimes a consorting male was replaced by a higher-ranking male before sexual interactions could take place. Maintenance of the consortship was measured in proportion to time spent in consort and was ascribed to the consort partner that followed the other. If the consort pair did not move, the maintenance of the consort was ascribed to the consort partner that had been the follower in the preceding move. During focal animal sampling, we also noted events in which a consorted female approached (i.e. came near to 5m or less to) a male other than the consort partner (event sampling; Altmann 1974). Furthermore, using the instantaneous sampling method (interval: 1 min; Altmann 1974), we measured how much time males that were lower ranking than the male consort partner spent in "proximity" to a consort pair, i.e. not more than 10 m (when with the group) or 20 m (when away from the group) away.

When a female stayed in consort for 100 minutes or more (long consorts), focal animal sampling was continued for the rest of the day. From this day on, the female was followed from dawn to dusk until she was not consorted anymore. Sometimes two or three females engaged in long consorts simultaneously, so that only one or two females could be followed the whole day through. The other female/s was/were then followed for half a day. The average observation time during long consorts per female was 6.1 h/day. When more than one female was in long consort, all non-consorting females were followed only every second day. Focal animal sampling was interrupted every half hour to check the group for composition, activity and location.

Data Analysis

All data presented here concerning consortships and sexual interactions exclusively refer to the defined fertile phases of the observed ovarian cycles and to the four days surrounding the oestrogen peak in the two cycles in which a fertile phase could not be determined (see above). Thus, 11 cycles were included in the analysis (for female observation time see Table 1). Data for female MA was obtained only during half of the fertile phase, because on two of the four days the female moved away from the group and was lost by the observer. The fact that male behaviour varied between different cycles of the same female indicated to us that these cycles differed in quality and thus can be seen as independent events. Since cycles differed significantly for example in the time a female was monopolised by the dominant male, female mating patterns and strategies can be expected to be different in different cycles. We have nevertheless averaged data from different cycles of the same females where we do not explicitly compare different cycle-types with each other.

To test whether female attractivity differed individually, we looked at the proportion of time the group's dominant male maintained a consort with a female. We restricted analysis to this male, because he was the only one who could express his interest in females without constraints. We did also not include alpha-male HB into analysis, because he only temporarily joined group HA. Female "attractivity" parameters tested included female dominance rank, female parity status and female oestrogen levels. For comparison of parity status, females were classified into two parity categories: 1 = nulliparous and primiparous; 2 = multiparous. For females that had more than one ovarian cycle during the study period, the mean consort time of all cycles was used. The only exception occurred for hormone levels: since females can have significantly different hormone levels in different cycles, we related individual hormone levels of a given cycle to the proportion of consort time in this particular cycle.

To estimate the degree of male coercion, we looked at the frequency with which males forced females into copulation. We further looked at how dominant males responded to their female consort partner when she approached other males during the consort period.

To assess the degree of female mate choice, we looked at how active females were in soliciting males, how often they refused male attempts to engage in sexual interactions (attempts to inspect the female or to mount the female) and how they distributed solicitations over males of different dominance rank or residency status. Since females mate-guarded by dominant males were constrained in mate choice, we restricted analysis to those cycles in which females were not continuously consorted by alpha males throughout their fertile phase.

We classified males by dominance rank and residency status. All males that held alpha or beta rank position in their groups were classified as high-ranking males and all other males were called subordinate males. The second-ranking male of group HA, which had just joined the group at the beginning of the study, often left the group or stayed at the periphery. Thus, the third-ranking male often held the functional beta position and was therefore named beta male HA and categorised as high-ranking.

Female long-tailed macaques solicit sexual interactions to males by presenting their anogenital region (Zumpe & Michael, 1983). We included only those solicitations into the analysis, which occurred after the female had approached the male. Thus, soliciting was part of a female initiated sexual contact and not the reaction to the approach of a male. We calculated for each female the proportion of solicitations that aimed at high-ranking males and the proportion that aimed at subordinate males and tested these values against each other. For females with several cycles, we used the mean of all cycles. The same was done for resident versus non-resident males. We did not look at differences in the frequency of refusals in terms of rank or residency, because females may not be as free to refuse a male as they are to solicit a male, since all males are higher ranking than females and might harass the refusing female.

To test whether paternity was related to the rate of ejaculations a female had received from specific males, we counted the number of ejaculations a likely father had with a female and tested it against the mean number of ejaculates the female had received from other males. We also looked at the timing of ejaculations within the fertile phase by calculating the proportion of ejaculates a female had received from the likely father on each day of the fertile phase. We then tested for differences in these values between the different fertile days.

Specific tests and sample sizes are given with the results. We generally applied non-parametric tests with two-tailed probabilities and a significance level of 0.05. All statistic tests were conducted with SPSS 11.0 for Windows.

RESULTS

Female Reproductive Cycles

Seven of the eight study females showed ovarian activity (Table 1). In total, eleven cycles were observed, including six conception cycles, four ovulatory non-conception cycles and one anovulatory cycle. Fertile phases were spread over seven months and, with the exception of two cycles (cycle LA*, SA1; Fig. 2), did not overlap with each other. However, eight fertile phases,

Fig. 2

including all conception cycles, occurred within the first 3.5 months (Fig. 2). All females who conceived gave birth to an infant after a mean of 163 days $(SD = 3.1)$, counting from the last day of the fertile phase.

Consortships

Fig. 3

Females were consorted during all fertile phases, but with varying duration and varying number and identity of consort partners (Fig. 3). Cycles could be classified according to the proportion of time alpha males consorted a female during her fertile phase. In six out of eleven cycles, females were consorted by alpha males for on average 97% of the observation time (monopolisation cycles; range: 91−100% observation time). In all of these cycles, consortships were male maintained during 100% of the consort time. Monopolisation cycles could be classified again into those in which females were exclusively consorted by alpha male HA during their fertile phases (cycle SA*, KA2, KA3) and those in which they were consorted alternately by alpha male HA and alpha male HB (cycle CA*, SA1, FA*).

In the remaining five cycles, alpha males consorted females on average only during 26% of the fertile phase (non-monopolisation cycles; range: 0–56% observation time). These cycles differed from monopolisation cycles in that females had significantly more consort partners (average: 4.2 partners, range: 2–8 partners; Mann-Whitney-U Test: $U = 2.5$, $N_1 = 5$, $N_2 = 6$, $P = 0.017$) and spent significantly less time in consort in general (average: 75% observation time, range: 63–94% observation time; Mann-Whitney-U Test: $U = 0$, $N_1 = 5$, $N_2 = 6$, $P = 0.004$). Furthermore, in two of these cycles, consortships were partly maintained by the female alone (cycle MA*: 57% consort time; cycle KA1: 26.3% consort time).

Number of Mating Partners

Monopolisation cycles and non-monopolisation cycles differed from each other in the number of mating partners: during fertile phases of non-monopolisation cycles, females had a mean of 5.2 mating partners (range: 4–7 partners) and thus significantly more mating partners than during monopolisation cycles (mean: 2.7 partners, range: 1–5) partners; Mann-Whitney-U Test: $U = 2.5$, $N_1 = 5$, $N_2 = 6$, $P = 0.017$). Although females in five of the monopolisation cycles had more than one mating partner, most copulations occurred with alpha males (mean: 93.4%, range: 81.3−100% copulations).

Female status and monopolisation by the dominant male

The proportion of time females were consorted by the group's alpha male during the fertile phase did not depend on female parity (Mann-Whitney-U Test: $U = 6$, $N_1 = 3$, $N_2 = 4$, $P > 0.99$). Time in consort with the alpha-male was also neither related to mean cycle oestrogen levels (Spearman rank correlation: $rs = -0.07$, $N = 11$, $P = 0.84$), nor to the mean oestrogen: progestogen ratio of cycles (Spearman rank correlation: $rs = 0.31$, $N = 11$, $P = 0.35$). We found however a significant correlation between female dominance rank and the time with which females were consorted by the group's alpha-male, with high-ranking females being consorted for longer periods than low-ranking females (Spearman rank correlation: $rs = 0.86$, $N = 7$, $P = 0.014$, Fig. 4).

Fig. 4

Male coercion and female mate choice

During the whole observation period, we observed 19 cases (2.5% of all refusals) involving six of the seven cycling females in which a female refused to mate, but was forcedly pulled into the right position and mounted by the male. Of these copulations, 82.4% terminated in ejaculation. In five monopolisation cycles, we observed that dominant males chased their female consort partner away from other males (30.1% of all cases in which a female approached a male other than the consort partner). Only twice (7.7% of all approaches) was a female observed to solicit mating with a non-dominant male while being consorted by a dominant male.

In non-monopolisation cycles in which females were not monopolised by males throughout the entire fertile phase, females showed a low degree of soliciting behaviour and a high degree of sexual permissiveness: a mean of 19.5% of all sexual interactions (range: 3.3–33.3% sexual interactions) occurred after female solicitations and on average only 18.7% of male sexual approaches (inspection and mounting attempts; range: 9.5–37.5% of male approaches) were refused by females. Furthermore, after almost half of these refusals, females were approached again and mated with the refused male within the next 10 minutes (mean: 44.6%, range: 14.3−100% of refusals).

Female mate choice was never restricted to a single male in non-monopolisation cycles and females solicited on average to 3.6 males (range: 2–6 males). There was further no significant preference for males of certain dominance rank or residence status in these cycles, neither for (A) high-ranking males in comparison to subordinate males nor for (B) non-resident versus resident males (Wilcoxon matched-pairs signed-ranks test: A: $Z = -1{,}1$, $N = 5$, $P = 0.27$, B: $Z = 0.0$, $N = 5$, $P > 0.99$).

Behaviour of Subordinate Males

Although alpha males that were consorting a female sometimes attacked subordinate males that were in proximity to the consort pair, subordinate males were observed in proximity to alpha males and their consort partner on average for 25.4% of the consort time (range: 0–59.3% consort time). Nevertheless, the number of sneak copulations was very low: only two copulations with non-alpha males occurred while the female was consorted by an alpha male (see above). No coalition forming among subordinate males against consorting alpha males was observed.

Paternity and Copulation Rate

There was a clear relation between male rank and paternity: all six infants born during the study period were sired by high-ranking males (Fig. 3), one by alpha male HA, three by alpha male HB and one each by beta males HA and HB. At the same time, there was an overall significant relation between male dominance rank and copulation rate. Females mated more often with higher ranking males than with sub-ordinate males (Wilcoxon signed-ranks test: $Z = -2.0$, $N = 7, P = 0.041$). However, male ejaculation rate and timing of ejaculation was not related to paternity. Females had not received significantly more ejaculations from likely fathers than from other males (Wilcoxon signed-ranks test: $Z = 1.5$, $N = 5$, $P = 0.14$) and receipt of ejaculations from fathers was not concentrated to specific days of the fertile phase (Friedman test: $\chi^2 = 0.8$, $N = 5$, $K = 3$, $P = 0.85$; Fig. 5).

Fig. 5

DISCUSSION

Male dominance rank and reproductive success

The results presented here confirm previous findings of a study of several groups of long-tailed macaques in the same population that almost all infants are sired by alpha and beta males in this species (de Ruiter et al. 1994). Given that a strong positive correlation between male dominance rank and paternity has now been observed in multiple groups of wild long-tailed macaques during several years, it seems that a high reproductive skew in favour of high-ranking males is a consistent characteristic of this species, at least for populations living in their natural habitat. Furthermore, our data support earlier findings in macaques (e.g. *Macaca mulatta*: Stern & Smith 1984; *Macaca sylvanus*: Paul et al. 1993) that mating success is not necessarily a reliable measure of male reproductive success underlying the importance of genetic paternity analyses.

Fig. 6

In the following, we will discuss the causes of the reproductive skew observed in long-tailed macaques as can be concluded from our results (see also Fig. 6).

Mate guarding by dominant males

We demonstrated that monopolisation of fertile females by dominant males occurs in wild long-tailed macaques and that monopolisation is timed to the cycle's fertile phase and results in paternity supporting the priority of access to oestrus females model (Altman 1962). Three of the six infants conceived during our study were sired by alpha males during cycles in which these males mate guarded the female throughout the entire fertile phase and in which copulations with males other than alpha males accounted only for a minor proportion of copulations. Since in two conception cycles the group's dominant male shared mate guarding and mating with the dominant male of an adjacent group, paternity in these cases is likely to be determined post-copulatory (i.e. within the female reproductive tract). Sharing of mate guarding between alpha males of different groups has never been observed in this well studied population. Furthermore, it has never been reported that dominant long-tailed macaque males temporarily switch groups during the mating season (compare van Noordwijk 1985; van Noordwijk & van Schaik 1988, 2001; de Ruiter et al. 1994). We speculate that the alpha male HB was attracted by the higher number of cycling females in group HA compared to his own group (A. Engelhardt unpubl. data). We presume therefore that under different conditions, more infants would have been sired by the group's dominant male as a result of mate guarding.

Although mate guarding by dominant males regularly occurred, it was not observed in all cycles and three of these cycles without male monopolisation led to conception. This is surprising in view of male ability to recognise a female's fertile phase (Engelhardt et al. 2004) and our finding of little overlap of fertile phases in our study females. Two basic models of reproductive skew provide a possible explanation for a lack of monopolisation by dominant males. According to the concession model (Vehrencamp 1983; Johnstone et al. 1999; Kokko & Johnstone 1999), high-ranking males do not always monopolise access to females provided that these males benefit from the presence of subordinate males, for example for group defence. The limited control model (Cant 1998; Clutton-Brock 1998; Reeve et al. 1998) on the other hand suggests that dominant males sometimes fail to monopolise access to females due to an assortment of factors such as female cycle synchrony, alternative male reproductive strategies or female choice. Our data does not allow to differentiate between both models for our study group. On one hand, the fact that the dominant male did not try to monopolise all females although theoretically possible supports the concession model. On the other hand, he might have disregarded some of the cycles in order to save time and energy for fighting competitors or to regenerate depleted energy reserves. Mate guarding is time and energy consuming (Alberts et al. 1996) and males should refrain from mate guarding when energetic demands are high and the available female is not of high interest (Alberts et al. 2003; Kappeler & van Schaik 2004). Given the rapid sequence with which fertile phases seem to occur in long-tailed macaques, males are from an energetic point of view possibly not able to monopolise all reproducing females during a complete mating season and, thus, might distribute mate-guarding efforts unevenly over different females. Our findings suggest that males prefer high-ranking females for consort (although we cannot not exclude that other factors than dominance rank also influenced male behaviour since our sample size was small). That dominant males prefer high-ranking females as reproductive partners is a common finding in primates (e.g. reviewed in Robinson 1982; Berenstain & Wade 1983; see also Kuester & Paul 1996), and makes perfect sense given the fact that high-ranking females often have a higher lifetime reproductive success than low-ranking females (reviewed in Silk 1987, Ellis 1995; for long-tailed macaques see van Noordwijk 1999). However, further studies will be needed to identify the costs and limitations of mate-guarding in long-tailed macaques and to clarify whether dominant males benefit from the presence of subordinate males.

The potential of post-copulatory mechanisms for determining paternity

We first show in wild long-tailed macaques, that polyandrous mating does not only occur during infertile periods of the female's ovarian cycle but also to a significant extent when conception is most likely. In the majority of cycles, including almost all conception cycles, polyandrous mating occurred to a significant extent during the fertile phase. Polyandrous mating during the fertile phase opens up the opportunity for sperm competition and female cryptic choice. From our data it seems that neither the number of ejaculations a female received from a male nor the timing of ejaculation affected male reproductive success (although these results should be taken cautiously due to the limited data set). Thus, in our study, paternity seems to almost exclusively been determined by mechanisms operating on the post-copulatory level. According to our data, two factors seem to affect the potential for post-copulatory paternity determination: stability of the alpha male position and male interest in females (Fig. 6). Given the special situation in our study group (see above: the dominant male of one of the adjacent groups temporarily joined it), the degree to which paternity was determined on the post-copulatory level might have been overestimated and male monopolisation may generally play a more important role. However, since three infants were conceived during cycles in which dominant males were just not interested in the female (as indicated by low rates of alpha male consortship), paternity determination within the female reproductive tract can be expected to occur to a significant extent even when only a single dominant male is with a group. A study on Hanuman langurs also provides clear evidence for the existence of post-copulatory paternity assignment (Heistermann et al., 2001) and the potential for it seems to be apparent in the majority of primate species. As in birds, repeated copulation, male mate-guarding and relatively large testes occur frequently in primates, traits that have been interpreted as adaptations to sperm competition. Furthermore, the interspecific variation found in the morphology of male primate genitalia and sperm may be functionally related to sperm competition (for a review see Birkhead & Kappeler 2004). More studies focusing on the period within a female cycle in which copulation can lead to conception are needed in order to evaluate the extent to which post-copulatory selection actually plays a role within the primates.

Female mate choice and alternative male reproductive strategies

The degree to which female mate choice contributed to paternity seemed to be low in our study group. During cycles in which females were monopolised by dominant males, mate choice was restricted through the harassment of the consorting male. We can, however, not exclude the possibility that mate-guarding by the alpha-male was not only based on coercion, but also on female cooperation. It has been suggested that primate females living in multi-male groups should concentrate mating to the dominant male in order to get protection from this male for the coming offspring (van Schaik et al. 1999). Females in our study were however not reluctant to mate with other males during the time they were in consort with the alpha-male. Furthermore, the observation that this male was able to force copulations and to chase female consort partners away from other males suggests that monopolisation of females does not necessarily need female cooperation.

Even when females were not monopolised, the proportion with which females solicited or refused sexual interactions was low. As a result, females were usually mating with several males during the fertile phase. Males, on the other hand, were insisting and often succeeded in mating with a female that had rejected the same male just a few minutes before. It can be assumed that female long-tailed macaques are sexually permissive in order to avoid harassment, since males are significantly bigger than females (Plavcan & van Schaik 1997), have much bigger canines (Plavcan & van Schaik 1992) and generally dominate females (Angst 1975). In fact, we have observed forced copulations several times, but the frequency was very low. Sexual harassment thus seems to be relatively rare in this species (see also Engelhardt et al. 2005), which might result from female permissiveness.

In addition to a low degree of initiative, females did not show any mate preference concerning male rank or residency. Our observations confirm results of a recent pair choice test, in which female long-tailed macaques most often mated with both available males during the fertile phase, irrespective of the combination of males presented (Nikitopoulos et al. in press). We therefore conclude that there is a low degree of female mate choice in long-tailed macaques, not only due to constraints set by males, but also to a lack of choosiness in the females. Instead females seem to aim at mating with several males, possibly to receive the benefits of polyandrous mating and sperm competition. These potential benefits (reviewed in Wolff & Macdonald 2004) include avoiding inbreeding or genetic incompatibilities (Newcomer et al. 1999; Zeh & Zeh 2001; Tregenza & Wedell 2002), reducing the risk of infanticide through paternity confusion (Hrdy 1979; van Schaik et al. 2000; Heistermann et al. 2001), enhancing paternal care (Taub 1980, but see Soltis & McElreath 2001), receiving good sperm ('good-sperm' model; Yasui 1997) and facilitating cryptic female choice (Eberhard 1996). It may however be that female long-tailed macaques follow two different strategies according to their situation: cooperating with the dominant male when he is interested in the female and increasing polyandrous mating when not. In addition, females may indirectly influence with whom they mate by supporting or opposing males that try to join the group (indirect female choice; Small 1989).

Our paternity data and that of de Ruiter and colleagues (1994) suggest that alternative male reproductive strategies play no or at least only a minor role for male reproductive success in long-tailed macaques. Subordinate males often followed a consorting pair and sometimes even managed to mate with a guarded female, but none of these copulations resulted in paternity. Two questions arise from the observed behaviour of subordinate males. First, why did subordinate males refuse to form coalitions against mate guarding dominant males. There may be two explanations to this question. First of all, Henzi et al. (1999) argue that small groups afford fewer opportunities for coalition formation and thus there is weaker selection on the behavioural tendency to form social alliances that might lead to coalitions. This may also apply to long-tailed macaques, in which group size and number of males within groups are small compared to other catarrhine primate multi-male groups. Furthermore, male bonnet macaques (*Macaca sinica*: Silk 1993) and Barbary macaques (*Macaca sylvanus*: Widdig et al. 2000), species in which coalition formation among males is common, rarely form coalitions against higher-ranking opponents to avoid retaliation. So it seems that the reluctance to form coalitions against males of higher status is a general pattern amongst macaques. The second question that remains to be answered is, why were females not continuously consorted during the fertile phase when not mate guarded by dominant males. This may be explained by the observation that consorting subordinate males were often supplanted by higher-ranking males and that females often mated with males higher ranking than their current consort partner. Thus, since subordinate males were not able to exclude other males from mating with the female, they may have decided to not invest more time and energy in mate-guarding the female.

Determinants of male reproductive success in wild long-tailed macaques

Collectively, our data suggest that predominantly both male monopolisation of females during their fertile phase and post-copulatory mechanisms determine male reproductive success in long-tailed macaques. It seems that our findings can be generalised at least to those long-tailed macaques living in their natural habitat, because they are supported by specific species characteristics. A pronounced sexual dimorphism in body and canine size (Plavcan & van Schaik 1992, 1997), moderately seasonal reproduction (Kavanagh & Laurensen 1984; van Schaik & van Noordwijk 1985), male ability to discern the fertile phase of a cycle (Engelhardt et al. 2004) and higher mating success in high-ranking males (van Noordwijk 1985; de Ruiter et al. 1994) all suggest a high degree of male monopolisation in this species. In contrast, a high testis to body weight ratio (Harcourt et al. 1981) and a high number of viable sperm in male ejaculates (Schrod 2002) point to a high degree of sperm competition.

Female mate choice and alternative male reproductive strategies, in contrast, did not directly affect male reproductive success. It may however be that females cooperated in monopolisation by the dominant male. Although paternity determination mostly occurred within the female reproductive tract in this study, infants were exclusively sired by alpha and beta males. This did obviously not result from higher ejaculation rates in likely fathers or from a specific timing of ejaculations within the fertile phase. Hence, although our sample size is limited, it seems that in long-tailed macaques, dominant males have an advantage in sperm competition, which might contribute to the high reproductive skew observed in this species. However, our knowledge on post-copulatory mechanisms is still limited (reviewed in Birkhead & Kappeler 2004). Clearly more investigations are needed for a better understanding of the processes leading to fertilisation within the female reproductive tract, and thus, of the proximate mechanisms determining paternity in primate multi-male groups.

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Table 1 Dominance rank, parity and number of ovarian cycles of study females. Observation time refers to the period a female was observed as focal animal during each of the fertile phases.

Study-female	Rank	Parity	Non-conception cycles	Conception cycles	Observation time (min)
SA	1	primiparous	2	1	1180/1564/1712
FA	2	nulliparous	0	1	1430
KA	3	multiparous	3	0	2262/1352/1966
AA	4	multiparous	0	1	1313
LA	5	multiparous	0	1	659
CA	6	multiparous	0	1	1585
MA	7	nulliparous	0	1	648
IA	8	multiparous	0	0	

Fig. 1 Faecal oestrogen and progestogen profile in an individual female long-tailed macaque (SA). The fertile phase was defined to be the days -2 to -5 from the day of rise in progestogen levels (day 0) above a certain threshold (for more details, see methods).

Fig. 2 Distribution of the fertile phases over the study period. Black bars indicate the fertile phase of conception cycles, hatched bars those of ovulatory non-conception cycles and the open bar indicates those days of the anovulatory cycle that were included into the analyses. Grey lines mark days with full consortship and the arrow indicates the period in which the alpha male of the adjacent group HB joined group HA.

Fig. 3 Proportion of observation time females spent in consortship with alpha male HA (black bars), with alpha male HB (black bars with cross-hatching) and with other males (white bars) during the fertile phase. Values given show the number of non-alpha consort partners, if more than one. Conception cycles are marked by asterisks, non-conception cycles are numbered by occurrence. Likely fathers are stated above the conception cycles.

Fig. 4 Proportion of observation time females spent in consortship with alpha male HA in relation to female dominance rank. The figure shows mean values for females that had more than one ovarian cycle.

Fig. 5 Proportion of ejaculates females received from likely fathers on a given day of the fertile phase. Since observation of female MA was not continuous, her data are not presented.

Fig. 6 Mechanisms leading to male reproductive success depending on i) recognisability of the fertile phase, ii) male dominance over females, iii) monopolisability of females and iv) mating modus. Gray arrows indicate the factors influencing male reproductive success in this study.

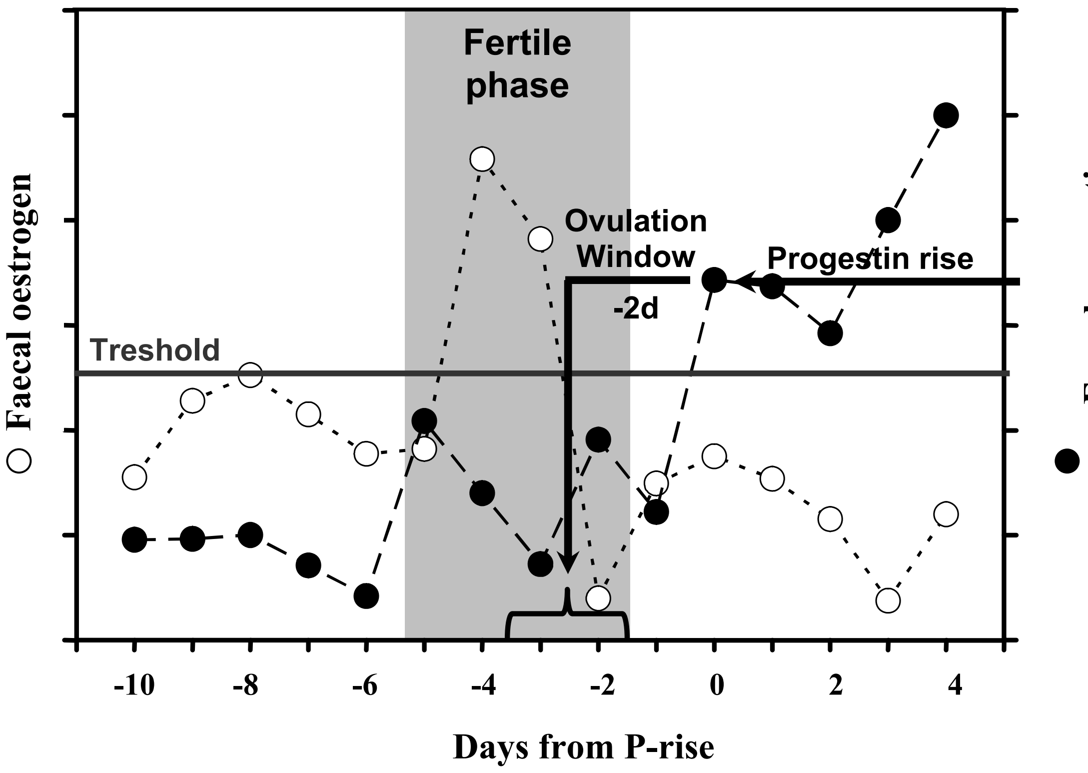

Fertile phase
Ovulation Window
-2d
Progestin rise
Treshold
○ Faecal oestrogen
Faecal progestin ●
-10
-8
-6
-4
-2
0
2
4
Days from P-rise

Fig.1

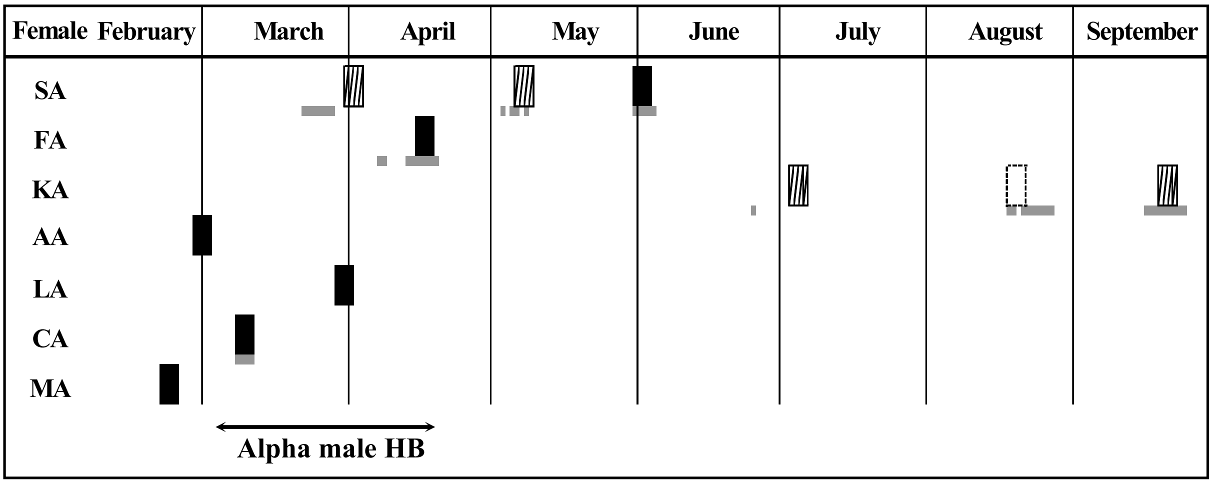
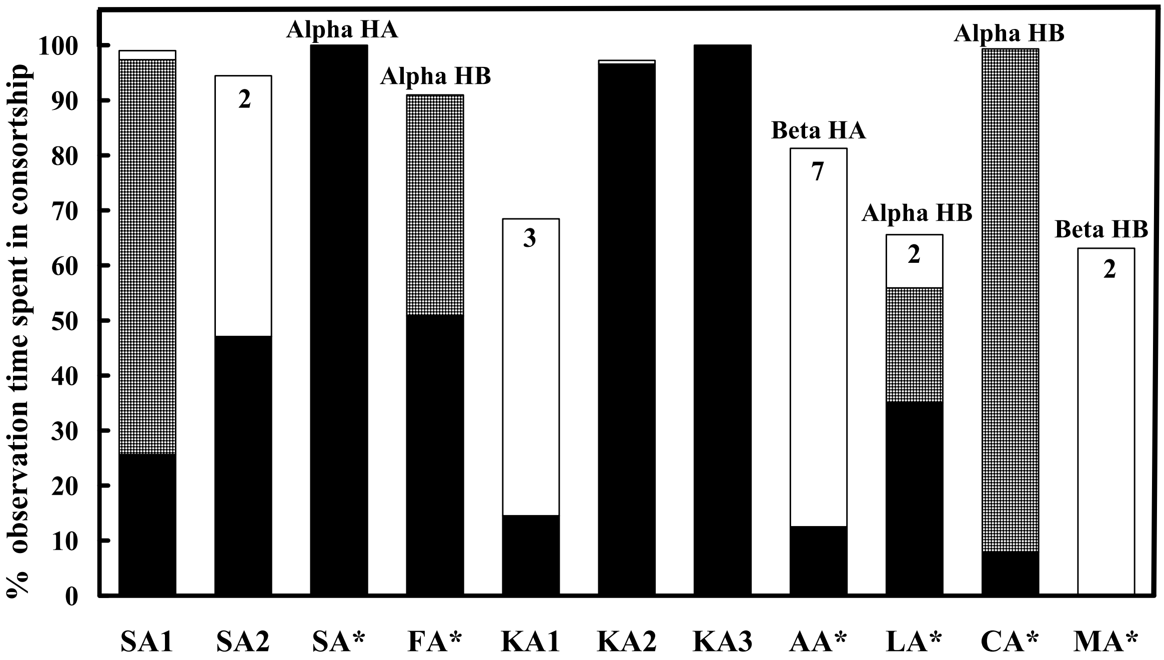

Female
February
March
April
May
June
July
August
September
SA
FA
KA
AA
LA
CA
MA
Alpha male HB

Fig. 2



% observation time spent in consortship
0
10
20
30
40
50
60
70
80
90
100
Alpha HA
Alpha HB
Beta HA
Alpha HB
Alpha HB
Beta HB
2
3
7
2
2
SA1
SA2
SA*
FA*
KA1
KA2
KA3
AA*
LA*
CA*
MA*

Fig. 3

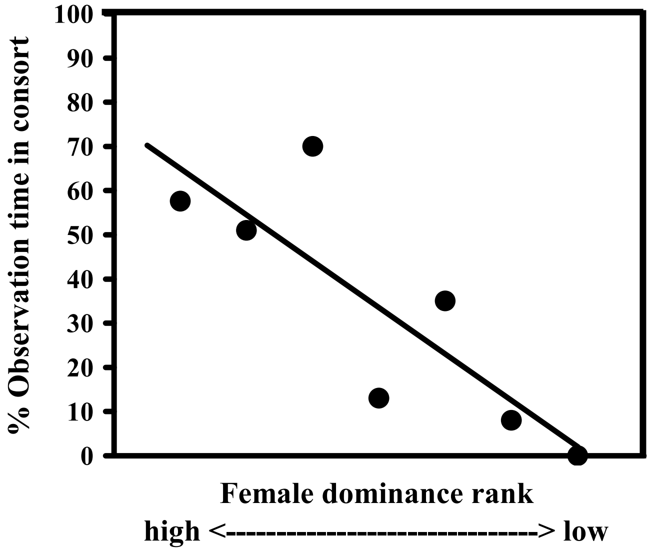

100
90
80
70
60
50
40
30
20
10
0
% Observation time in consort
Female dominance rank
high <-------------------------------> low

Fig. 4

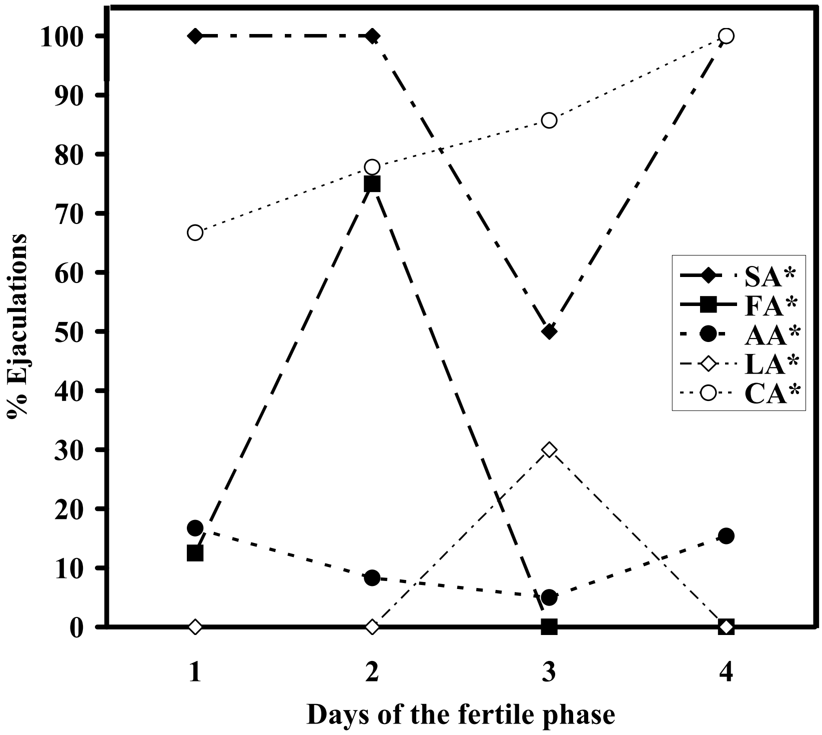

% Ejaculations
100
90
80
70
60
50
40
30
20
10
0
1
2
3
4
Days of the fertile phase
SA*
FA*
AA*
LA*
CA*

Fig. 5

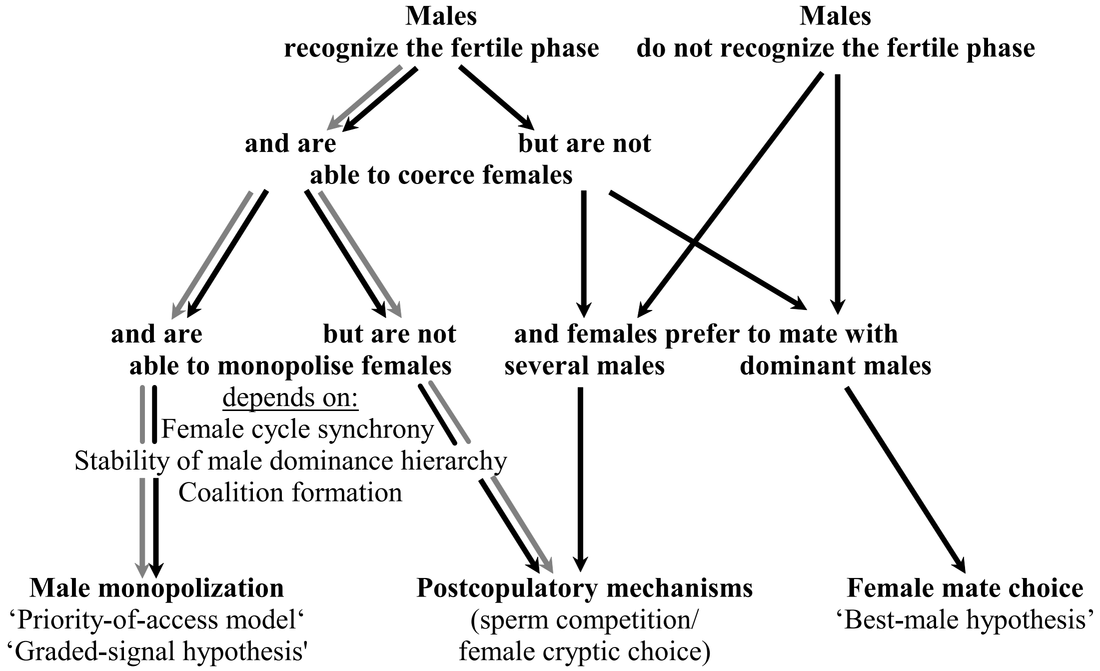

Males
recognize the fertile phase
Males
do not recognize the fertile phase
and are
but are not
able to coerce females
and are
but are not
able to monopolise females
depends on:
Female cycle synchrony
Stability of male dominance hierarchy
Coalition formation
and females prefer to mate with
several males
dominant males
Male monopolization
'Priority-of-access model'
'Graded-signal hypothesis'
Postcopulatory mechanisms
(sperm competition/
female cryptic choice)
Female mate choice
'Best-male hypothesis'

Fig. 6