

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

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## 26 **Abstract**

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

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

49

## **INTRODUCTION**

50 A fundamental question in primate sexual selection concerns the proximate mechanisms  
51 underlying male reproductive success in multi-male groups. According to sexual selection  
52 theory, males should compete for access to receptive females, the resource that limits male  
53 reproductive success the most (Trivers 1972). Contest among males for access to mates, in turn,  
54 should lead to social systems in which the strongest male is able to monopolise access to fertile

55 females (priority of access to oestrus females model: Altmann 1962; see also Fedigan 1983). The  
56 finding that dominant males often sire the majority of offspring clearly shows that dominance  
57 plays an important role for male reproductive success in mammals (Ellis 1995), including  
58 primates (e.g. *Cercocebus torquatus atys*: Gust et al. 1998; *Macaca sylvanus*: Paul & Kuester  
59 1996; *Mandrillus sphinx*: Dixson et al. 1993; *Papio cynocephalus*: Altmann et al. 1996).  
60 Complete monopolisation of females is, however, difficult to achieve. In some primate species,  
61 subordinate and extra-group males have a significant share in paternity (e.g. *Macaca fuscata*:  
62 Inoue et al. 1993; Soltis et al. 2001; *Macaca mulatta*: Berard et al. 1993, 1994; Widdig et al.  
63 2004), which indicates that other mechanisms operate as well in determining paternity. Thus, the  
64 importance of female and alternative male reproductive strategies as well as the interactive  
65 aspects of these has become increasingly recognised in recent years (e.g. Taub 1980; Janson  
66 1984; Small 1989; Manson 1994; Bercovitch 1995; Chism & Rogers 1997; Sterck et al. 1997;  
67 Soltis et al. 2000, 2001, 2004).

68 Successful monopolisation of access to fertile females depends on several factors (reviewed in  
69 Soltis 2004). One of these factors is synchrony of female ovarian cycles, because males are  
70 hardly able to successfully monopolise more than one female at a time (Paul 1997, Nunn 1999a).  
71 Fighting ability as well as coalition forming of subordinate males are also important  
72 determinants of male mating and mate guarding success, as has been shown for savannah  
73 baboons (*Papio cynocephalus*; Packer 1977; Bercovitch 1986; Noë & Sluijter 1990; Alberts et al.  
74 2003). A third variable that may influence monopolisation of females is the degree to which  
75 females resist or cooperate with males (Bercovitch 1995) and it seems that in at least some  
76 primate species, females are able to resist mating attempts (e.g. *Macaca mulatta*, Manson 1992;  
77 see also Soltis 2004).

78 Females should pursue reproductive strategies for their own best fitness increase. These  
79 strategies could also be opposing to male reproductive interests leading to inter-sexual conflict  
80 over control of reproduction (e.g. Trivers 1972; Smuts & Smuts 1993; Clutton-Brock & Parker  
81 1995; Gowaty 1996; Nunn & van Schaik 2000). Whether females are able to exert their own  
82 reproductive strategies, however, depends on the ability and degree of male coercion. Mate  
83 guarding by dominant males may be one of the strongest forms of male coercion if it is not based  
84 on female cooperation.

85 Whereas probability of paternity is affected on the pre-copulatory level (Paul 2002) (i.e. the level  
86 on which a behaviour can increase or decrease the probability of mating between two individuals) by

87 male monopolisation and female mate choice, it will be affected on the post-copulatory level  
88 whenever mating is not concentrated on a single male during the fertile phase. As soon as several  
89 males mate with the same female during her fertile phase, sperm of the different males will  
90 compete for fertilisation and paternity will be determined within the female reproductive tract.  
91 The number and viability of sperm a male brings into competition has, in this respect, been  
92 suggested to markedly affect his chances of siring offspring (reviewed in Birkhead & Møller  
93 1998; see also Birkhead 2000). It may also be that the female controls which male will fertilise  
94 her oocyte by, for example, discarding or destroying sperm from unfavoured males (cryptic  
95 female choice; reviewed in Eberhard 1996; Reeder 2003). It remains largely unknown to what  
96 extent post-copulatory selection of sperm from a particular male plays a role for male  
97 reproductive success in multi-male primate groups, although the potential for it seems to be  
98 apparent in the majority of primate species (Birkhead & Kappeler 2004).

99 Which of the pursued reproductive strategies eventually comes into effect leading to paternity  
100 depends on the events occurring during the female's fertile phase, i.e. the brief period within a  
101 female ovarian cycle when copulation can lead to conception. Since the objective assessment of  
102 female reproductive status was for a long time impossible in the wild, conclusions about primate  
103 reproductive strategies were mainly based on observations conducted over almost the whole  
104 female cycle. If studies were focused on the fertile phase, assessment of this period had to rely  
105 on secondary markers like sexual swellings that have only limited value (Nunn 1999b, Reichert  
106 2002, Deschner 2003, Engelhardt et al. 2005). Recent studies, however, have shown that male  
107 and female reproductive behaviour can vary significantly according to the stage of the female  
108 cycle (Deschner et al. 2004; Stumpf & Boesch 2005). In this respect, concealment of the fertile  
109 phase has been interpreted as a female strategy to hamper mate guarding in order to achieve  
110 more freedom for own reproductive decisions (van Schaik et al. 2000; Heistermann et al. 2001).  
111 If the probability of ovulation is only gradually but not precisely signalled (graded-signal  
112 hypothesis; Nunn 1999b), females might be able to mate polyandrously with subordinate males  
113 during times with low (but not zero) probability of conception and to attract dominant males  
114 during times of higher probability. The ability to recognise the female fertile phase, on the  
115 contrary, can significantly affect male reproductive success. Since monopolisation of females is  
116 costly (Alberts et al. 1996), males benefit from discerning the fertile phase of a cycle by being  
117 able to restrict mating efforts and mate guarding to this period. Recognition of the fertile phase

118 seems to occur at least to some degree in some primate species (*Macaca fascicularis*; Engelhardt  
119 et al. 2004; but see *Trachypithecus entellus*: Heistermann et al. 2001).

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

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## METHODS

### 135 **Animals and Study Site**

136 The study was carried out at the Ketambe Research Station (3°41'N, 97°39'E), Gunung Leuser  
137 National Park, North Sumatra, Indonesia. The research area consists of primary lowland  
138 rainforest and has been described by Rijksen (1978) and van Schaik & Mirmanto (1985).  
139 Behavioural observations and faecal sample collection occurred from February 14 until  
140 December 16, 2000.

141 The long-tailed macaques of the study area have been studied since 1979 and were well  
142 habituated to observers. The study focused on the group "House Atas" (HA). This group was one  
143 of three daughter groups ("House Atas", "House Bawah", HB, and "House Dapur", HD) of the  
144 former House group (B. Putragayo, pers. comment). At the beginning of the study, group HA  
145 consisted of eight adult females, five adult males and several subadults/juveniles and two infants.  
146 The home range of group HA overlapped with that of groups HB and HD and further with that of  
147 a third group, the Ketambe Bawah group (KB). Males from all adjacent groups and, in addition,  
148 those from a fifth nearby group (group "Antara") entered the home range of group HA from time

Tab. 1

149 to time and engaged in sexual interactions with females. The alpha male of group HB (alpha  
150 male HB) joined the group HA almost daily from beginning of March 2000 until mid-April 2000  
151 (Fig. 2), but returned every night to sleep with his own group. All group members of the study  
152 group HA and all males that moved within the home range of HA, were individually known.

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### 155 **Hormone Analysis and Definition of the Fertile Phase**

156 Faecal hormone extraction and analysis conducted for assessment of female cycle stage and  
157 timing of the fertile phase has already been described (details in Engelhardt et al. 2004). Briefly,  
158 2–3 g faeces were collected from each adult female (Table 1) on four to seven days per week and  
159 stored in 15 ml absolute ethanol at 4°C until hormone analysis. Extracts were measured for  
160 concentrations of immunoreactive oestrogen (total oestrogens, iEtotal) and progestogen  
161 (pregnanediol-3-glucuronide, iPdG) metabolites. Both measurements have been shown to  
162 provide reliable information on female ovarian function and timing of ovulation in long-tailed  
163 macaques (Shideler et al. 1993; Engelhardt et al. 2004).

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

173 Two cycles differed from the other cycles in that in one (KA2) ovulation did not occur (as  
174 indicated by lack of iPdG rise; in the cycle prior to and after this cycle the female did ovulate,  
175 Table 1), although female oestrogen levels were elevated and followed a normal pattern. In the  
176 other (SA1), oestrogen levels were elevated more than a week before the iPdG rise. In both  
177 cycles, however, female sexual activity and male interest in the female was increased during the  
178 period of elevated female oestrogen levels, as it was in normal ovulatory cycles. Since our earlier  
179 study showed that both female sexual activity and female attractivity to males are related to  
180 female oestrogen levels (Engelhardt et al. 2005) and since the pattern of male and female

**Fig. 1**

181 behaviour was comparable to that during the fertile phases of ovulatory cycles, we included data  
182 from the four days surrounding the day of maximum female oestrogen values into our  
183 behavioural analyses. The four days included started on day -2 relative to the day of maximum  
184 oestrogen value (day 0), which was on average the third day of the fertile phase during the  
185 regular ovulatory cycles.

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### 188 **Genetic Paternity Analysis**

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

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

208 We compared the mother and offspring genotypes to deduce which infant allele was inherited  
209 from the father. If the mother and infant had the same two alleles or if we were not able to  
210 genotype a mother at a certain locus, both infant alleles were considered as potential paternal  
211 alleles. Males who did not match with the deduced paternal alleles at anyone’s locus were

212 excluded from paternity. A male was considered the likely father, if (1) all other males were  
213 excluded from paternity, and (2) he was compatible with the paternal alleles in all genotyped loci  
214 (at least six). In only one case, no male matched with the deduced paternal alleles in all  
215 genotyped loci. In this case, the only male that had only one mismatch with the paternal alleles  
216 was assumed to be the likely father. We furthermore calculated parentage likelihood using the  
217 program CERVUS 2.0 (Tristan Marshall, Edinburgh, UK; Marshall et al. 1998) including only  
218 those alleles that matched our definition for 'true alleles'. All deduced paternities had a  
219 likelihood of  $\geq 98\%$ .

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## 222 **Behavioural Observations**

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

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



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

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

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

271

272

### 273 **Data Analysis**

274 All data presented here concerning consortships and sexual interactions exclusively refer to the  
275 defined fertile phases of the observed ovarian cycles and to the four days surrounding the

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

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

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

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

306 We classified males by dominance rank and residency status. All males that held alpha or beta  
307 rank position in their groups were classified as high-ranking males and all other males were

308 called subordinate males. The second-ranking male of group HA, which had just joined the  
309 group at the beginning of the study, often left the group or stayed at the periphery. Thus, the  
310 third-ranking male often held the functional beta position and was therefore named beta male HA  
311 and categorised as high-ranking.

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

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

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

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## RESULTS

### 334 Female Reproductive Cycles

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

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

342

343

### 344 **Consortships**

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

354 In the remaining five cycles, alpha males consorted females on average only during 26% of the  
 355 fertile phase (non-monopolisation cycles; range: 0–56% observation time). These cycles differed  
 356 from monopolisation cycles in that females had significantly more consort partners (average: 4.2  
 357 partners, range: 2–8 partners; Mann-Whitney-U Test:  $U = 2.5$ ,  $N_1 = 5$ ,  $N_2 = 6$ ,  $P = 0.017$ ) and  
 358 spent significantly less time in consort in general (average: 75% observation time, range: 63–  
 359 94% observation time; Mann-Whitney-U Test:  $U = 0$ ,  $N_1 = 5$ ,  $N_2 = 6$ ,  $P = 0.004$ ).  
 360 Furthermore, in two of these cycles, consortships were partly maintained by the female alone  
 361 (cycle MA\*: 57% consort time; cycle KA1: 26.3% consort time).

362

363

### 364 **Number of Mating Partners**

365 Monopolisation cycles and non-monopolisation cycles differed from each other in the number of  
 366 mating partners: during fertile phases of non-monopolisation cycles, females had a mean of 5.2  
 367 mating partners (range: 4–7 partners) and thus significantly more mating partners than during  
 368 monopolisation cycles (mean: 2.7 partners, range: 1–5) partners; Mann-Whitney-U Test:  
 369  $U = 2.5$ ,  $N_1 = 5$ ,  $N_2 = 6$ ,  $P = 0.017$ ). Although females in five of the monopolisation cycles

Fig. 3

370 had more than one mating partner, most copulations occurred with alpha males (mean: 93.4%,  
371 range: 81.3–100% copulations).

372

373

#### 374 **Female status and monopolisation by the dominant male**

375 The proportion of time females were consorted by the group's alpha male during the fertile phase  
376 did not depend on female parity (Mann-Whitney-U Test:  $U = 6$ ,  $N_1 = 3$ ,  $N_2 = 4$ ,  $P > 0.99$ ).

377 Time in consort with the alpha-male was also neither related to mean cycle oestrogen levels

378 (Spearman rank correlation:  $r_s = -0.07$ ,  $N = 11$ ,  $P = 0.84$ ), nor to the mean oestrogen:

379 progesterone ratio of cycles (Spearman rank correlation:  $r_s = 0.31$ ,  $N = 11$ ,  $P = 0.35$ ). We found

380 however a significant correlation between female dominance rank and the time with which

381 females were consorted by the group's alpha-male, with high-ranking females being consorted

382 for longer periods than low-ranking females (Spearman rank correlation:  $r_s = 0.86$ ,  $N = 7$ ,

383  $P = 0.014$ , Fig. 4).

384

385

#### 386 **Male coercion and female mate choice**

387 During the whole observation period, we observed 19 cases (2.5% of all refusals) involving six

388 of the seven cycling females in which a female refused to mate, but was forcibly pulled into the

389 right position and mounted by the male. Of these copulations, 82.4% terminated in ejaculation.

390 In five monopolisation cycles, we observed that dominant males chased their female consort

391 partner away from other males (30.1% of all cases in which a female approached a male other

392 than the consort partner). Only twice (7.7% of all approaches) was a female observed to solicit

393 mating with a non-dominant male while being consorted by a dominant male.

394 In non-monopolisation cycles in which females were not monopolised by males throughout the

395 entire fertile phase, females showed a low degree of soliciting behaviour and a high degree of

396 sexual permissiveness: a mean of 19.5% of all sexual interactions (range: 3.3–33.3% sexual

397 interactions) occurred after female solicitations and on average only 18.7% of male sexual

398 approaches (inspection and mounting attempts; range: 9.5–37.5% of male approaches) were

399 refused by females. Furthermore, after almost half of these refusals, females were approached

Fig. 4

400 again and mated with the refused male within the next 10 minutes (mean: 44.6%, range:  
401 14.3–100% of refusals).

402 Female mate choice was never restricted to a single male in non-monopolisation cycles and  
403 females solicited on average to 3.6 males (range: 2–6 males). There was further no significant  
404 preference for males of certain dominance rank or residence status in these cycles, neither for (A)  
405 high-ranking males in comparison to subordinate males nor for (B) non-resident versus resident  
406 males (Wilcoxon matched-pairs signed-ranks test: A:  $Z = -1.1$ ,  $N = 5$ ,  $P = 0.27$ , B:  $Z = 0.0$ ,  
407  $N = 5$ ,  $P > 0.99$ ).

408

409

#### 410 **Behaviour of Subordinate Males**

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

417

418

#### 419 **Paternity and Copulation Rate**

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

430

**Fig. 5**

431

432

## DISCUSSION

### 433 **Male dominance rank and reproductive success**

434 The results presented here confirm previous findings of a study of several groups of long-tailed  
435 macaques in the same population that almost all infants are sired by alpha and beta males in this  
436 species (de Ruiter et al. 1994). Given that a strong positive correlation between male dominance  
437 rank and paternity has now been observed in multiple groups of wild long-tailed macaques  
438 during several years, it seems that a high reproductive skew in favour of high-ranking males is a  
439 consistent characteristic of this species, at least for populations living in their natural habitat.  
440 Furthermore, our data support earlier findings in macaques (e.g. *Macaca mulatta*: Stern & Smith  
441 1984; *Macaca sylvanus*: Paul et al. 1993) that mating success is not necessarily a reliable  
442 measure of male reproductive success underlying the importance of genetic paternity analyses.

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

445

446

### 447 **Mate guarding by dominant males**

448 We demonstrated that monopolisation of fertile females by dominant males occurs in wild long-  
449 tailed macaques and that monopolisation is timed to the cycle's fertile phase and results in  
450 paternity supporting the priority of access to oestrus females model (Altman 1962). Three of the  
451 six infants conceived during our study were sired by alpha males during cycles in which these  
452 males mate guarded the female throughout the entire fertile phase and in which copulations with  
453 males other than alpha males accounted only for a minor proportion of copulations. Since in two  
454 conception cycles the group's dominant male shared mate guarding and mating with the  
455 dominant male of an adjacent group, paternity in these cases is likely to be determined post-  
456 copulatory (i.e. within the female reproductive tract). Sharing of mate guarding between alpha  
457 males of different groups has never been observed in this well studied population. Furthermore,  
458 it has never been reported that dominant long-tailed macaque males temporarily switch groups  
459 during the mating season (compare van Noordwijk 1985; van Noordwijk & van Schaik 1988,  
460 2001; de Ruiter et al. 1994). We speculate that the alpha male HB was attracted by the higher

Fig. 6

461 number of cycling females in group HA compared to his own group (A. Engelhardt unpubl.  
462 data). We presume therefore that under different conditions, more infants would have been sired  
463 by the group's dominant male as a result of mate guarding.

464 Although mate guarding by dominant males regularly occurred, it was not observed in all cycles  
465 and three of these cycles without male monopolisation led to conception. This is surprising in  
466 view of male ability to recognise a female's fertile phase (Engelhardt et al. 2004) and our finding  
467 of little overlap of fertile phases in our study females. Two basic models of reproductive skew  
468 provide a possible explanation for a lack of monopolisation by dominant males. According to the  
469 concession model (Vehrencamp 1983; Johnstone et al. 1999; Kokko & Johnstone 1999), high-  
470 ranking males do not always monopolise access to females provided that these males benefit  
471 from the presence of subordinate males, for example for group defence. The limited control  
472 model (Cant 1998; Clutton-Brock 1998; Reeve et al. 1998) on the other hand suggests that  
473 dominant males sometimes fail to monopolise access to females due to an assortment of factors  
474 such as female cycle synchrony, alternative male reproductive strategies or female choice. Our  
475 data does not allow to differentiate between both models for our study group. On one hand, the  
476 fact that the dominant male did not try to monopolise all females although theoretically possible  
477 supports the concession model. On the other hand, he might have disregarded some of the cycles  
478 in order to save time and energy for fighting competitors or to regenerate depleted energy  
479 reserves. Mate guarding is time and energy consuming (Alberts et al. 1996) and males should  
480 refrain from mate guarding when energetic demands are high and the available female is not of  
481 high interest (Alberts et al. 2003; Kappeler & van Schaik 2004). Given the rapid sequence with  
482 which fertile phases seem to occur in long-tailed macaques, males are from an energetic point of  
483 view possibly not able to monopolise all reproducing females during a complete mating season  
484 and, thus, might distribute mate-guarding efforts unevenly over different females. Our findings  
485 suggest that males prefer high-ranking females for consort (although we cannot not exclude that  
486 other factors than dominance rank also influenced male behaviour since our sample size was  
487 small). That dominant males prefer high-ranking females as reproductive partners is a common  
488 finding in primates (e.g. reviewed in Robinson 1982; Berenstein & Wade 1983; see also Kuester  
489 & Paul 1996), and makes perfect sense given the fact that high-ranking females often have a  
490 higher lifetime reproductive success than low-ranking females (reviewed in Silk 1987, Ellis  
491 1995; for long-tailed macaques see van Noordwijk 1999). However, further studies will be



492 needed to identify the costs and limitations of mate-guarding in long-tailed macaques and to  
493 clarify whether dominant males benefit from the presence of subordinate males.

494

495

#### 496 **The potential of post-copulatory mechanisms for determining paternity**

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

524

525

**526 Female mate choice and alternative male reproductive strategies**

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

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

548 In addition to a low degree of initiative, females did not show any mate preference concerning  
549 male rank or residency. Our observations confirm results of a recent pair choice test, in which  
550 female long-tailed macaques most often mated with both available males during the fertile phase,  
551 irrespective of the combination of males presented (Nikitopoulos et al. in press). We therefore  
552 conclude that there is a low degree of female mate choice in long-tailed macaques, not only due  
553 to constraints set by males, but also to a lack of choosiness in the females. Instead females seem  
554 to aim at mating with several males, possibly to receive the benefits of polyandrous mating and  
555 sperm competition. These potential benefits (reviewed in Wolff & Macdonald 2004) include

556 avoiding inbreeding or genetic incompatibilities (Newcomer et al. 1999; Zeh & Zeh 2001;  
557 Tregenza & Wedell 2002), reducing the risk of infanticide through paternity confusion (Hrdy  
558 1979; van Schaik et al. 2000; Heistermann et al. 2001), enhancing paternal care (Taub 1980, but  
559 see Soltis & McElreath 2001), receiving good sperm ('good-sperm' model; Yasui 1997) and  
560 facilitating cryptic female choice (Eberhard 1996). It may however be that female long-tailed  
561 macaques follow two different strategies according to their situation: cooperating with the  
562 dominant male when he is interested in the female and increasing polyandrous mating when not.  
563 In addition, females may indirectly influence with whom they mate by supporting or opposing  
564 males that try to join the group (indirect female choice; Small 1989).

565 Our paternity data and that of de Ruiter and colleagues (1994) suggest that alternative male  
566 reproductive strategies play no or at least only a minor role for male reproductive success in  
567 long-tailed macaques. Subordinate males often followed a consorting pair and sometimes even  
568 managed to mate with a guarded female, but none of these copulations resulted in paternity. Two  
569 questions arise from the observed behaviour of subordinate males. First, why did subordinate  
570 males refuse to form coalitions against mate guarding dominant males. There may be two  
571 explanations to this question. First of all, Henzi et al. (1999) argue that small groups afford fewer  
572 opportunities for coalition formation and thus there is weaker selection on the behavioural  
573 tendency to form social alliances that might lead to coalitions. This may also apply to long-tailed  
574 macaques, in which group size and number of males within groups are small compared to other  
575 catarrhine primate multi-male groups. Furthermore, male bonnet macaques (*Macaca sinica*: Silk  
576 1993) and Barbary macaques (*Macaca sylvanus*: Widdig et al. 2000), species in which coalition  
577 formation among males is common, rarely form coalitions against higher-ranking opponents to  
578 avoid retaliation. So it seems that the reluctance to form coalitions against males of higher status  
579 is a general pattern amongst macaques. The second question that remains to be answered is, why  
580 were females not continuously consorted during the fertile phase when not mate guarded by  
581 dominant males. This may be explained by the observation that consorting subordinate males  
582 were often supplanted by higher-ranking males and that females often mated with males higher  
583 ranking than their current consort partner. Thus, since subordinate males were not able to  
584 exclude other males from mating with the female, they may have decided to not invest more time  
585 and energy in mate-guarding the female.

586

587

## 588 **Determinants of male reproductive success in wild long-tailed macaques**

589 Collectively, our data suggest that predominantly both male monopolisation of females during  
590 their fertile phase and post-copulatory mechanisms determine male reproductive success in long-  
591 tailed macaques. It seems that our findings can be generalised at least to those long-tailed  
592 macaques living in their natural habitat, because they are supported by specific species  
593 characteristics. A pronounced sexual dimorphism in body and canine size (Plavcan & van Schaik  
594 1992, 1997), moderately seasonal reproduction (Kavanagh & Laurensen 1984; van Schaik & van  
595 Noordwijk 1985), male ability to discern the fertile phase of a cycle (Engelhardt et al. 2004) and  
596 higher mating success in high-ranking males (van Noordwijk 1985; de Ruiter et al. 1994) all  
597 suggest a high degree of male monopolisation in this species. In contrast, a high testis to body  
598 weight ratio (Harcourt et al. 1981) and a high number of viable sperm in male ejaculates (Schrod  
599 2002) point to a high degree of sperm competition.

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

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614

## **ACKNOWLEDGEMENTS**

615 We gratefully acknowledge the cooperation and support of the Indonesian Institute of Sciences  
616 (LIPI); the General Directorate of Forest Protection and Nature Conservation (PKA); the  
617 Universitas Nasional (UNAS), Jakarta (in particular Tatang Mitra Setia); and the Leuser  
618 Management Unit (UML). We thank the UML staff in Medan and Ketambe for providing an

619 excellent research environment and strong logistical support; Arwin, Azhar, Bahlias, Dewi,  
 620 Matplin, Rahimin, Samsu and Surya for assistance in the field; and Jutta Hagedorn and Andrea  
 621 Heistermann for laboratory assistance. Jan de Ruiter generously provided us with blood samples  
 622 from the Ketambe population for the establishment of microsatellite analysis in long-tailed  
 623 macaques and Heike Rösler conducted most of the genetic analysis. We thank Anja Widdig and  
 624 three anonymous reviewers for valuable comments on the manuscript. This research was  
 625 financed by the German Research Council (DFG) (Ni186/14-1). A. Engelhardt was financially  
 626 supported by the German Academic Exchange Service (DAAD), the State of Berlin Graduate  
 627 Sponsorship (Nafög), the KKGS Fund, the Lucie-Burgers Foundation for Comparative Research,  
 628 Arnhem, the Netherlands, and the Christian-Vogel-Funds. This study complies with the current  
 629 laws of the countries in which it was performed.

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840 **Table 1** Dominance rank, parity and number of ovarian cycles of study females. Observation  
 841 time refers to the period a female was observed as focal animal during each of the fertile  
 842 phases.  
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| Study-female | Rank | Parity      | Non-conception<br>cycles | Conception<br>cycles | Observation time<br>(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                    |                           |

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

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

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

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

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

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

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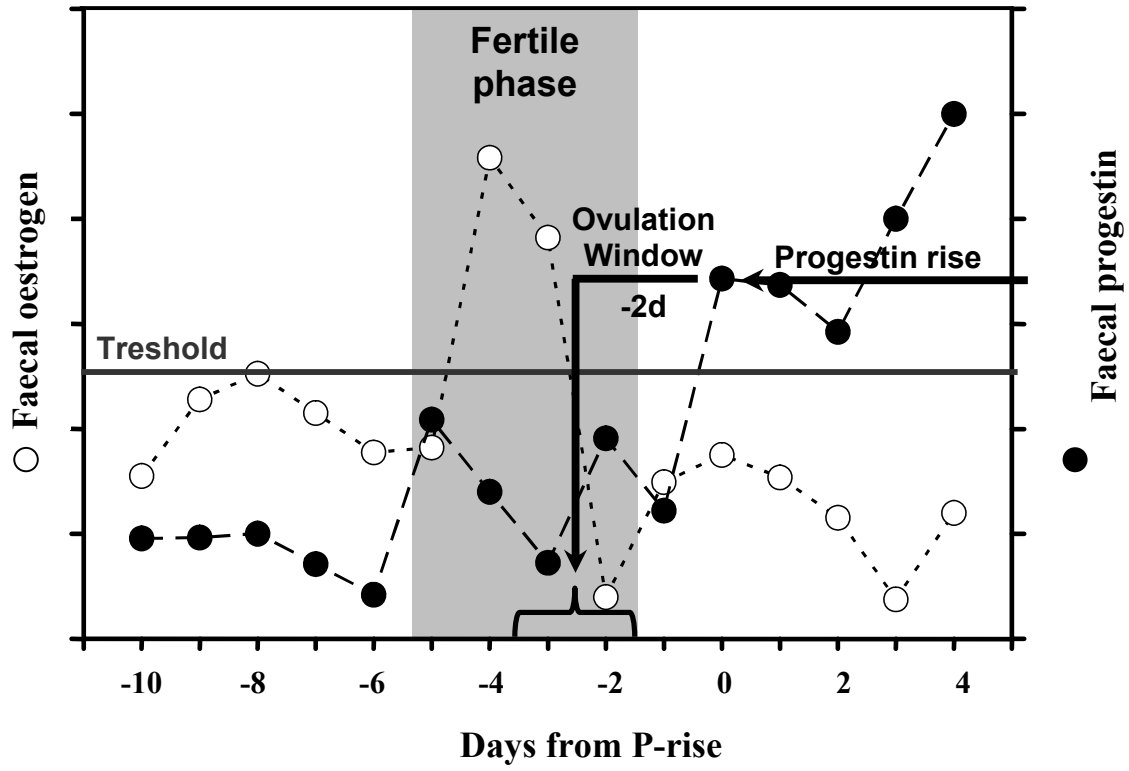
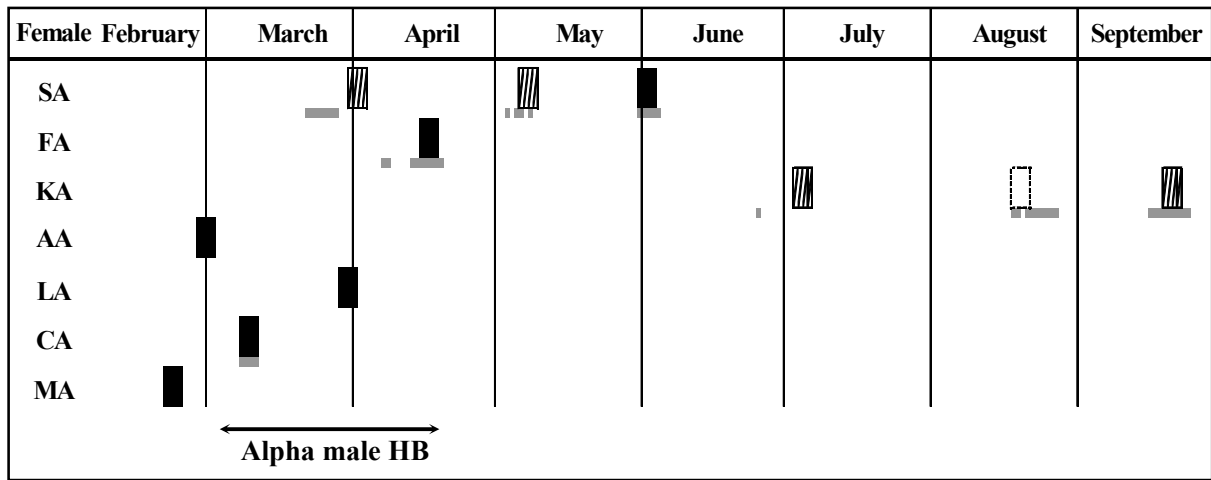


Fig.1

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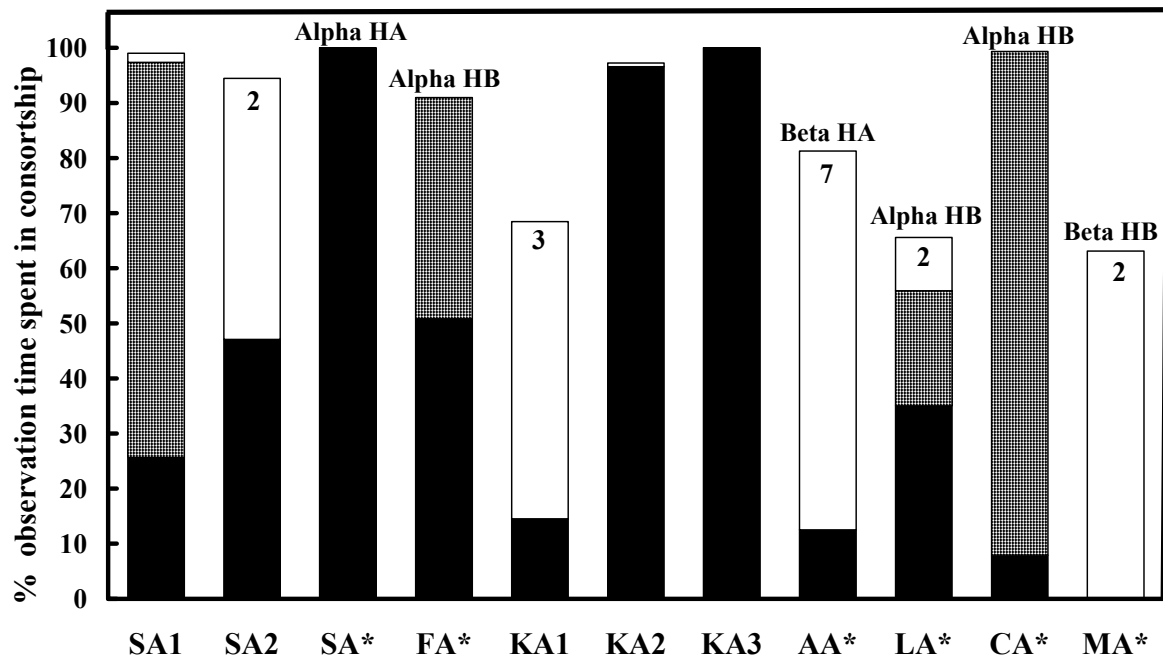
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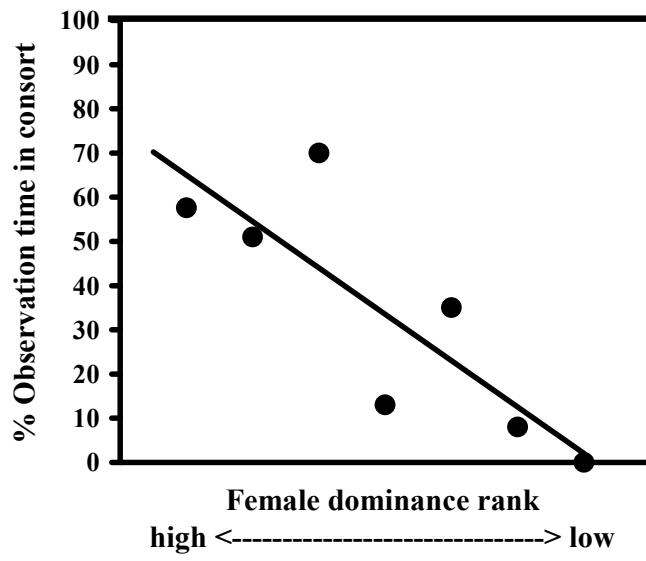
**Fig. 2**





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**Fig. 3**



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Fig. 4

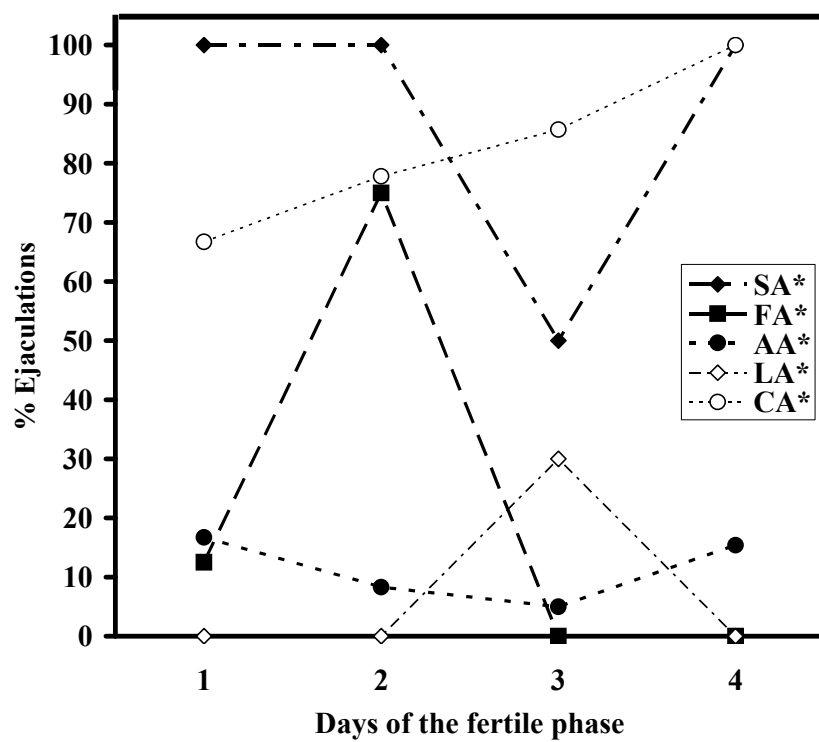
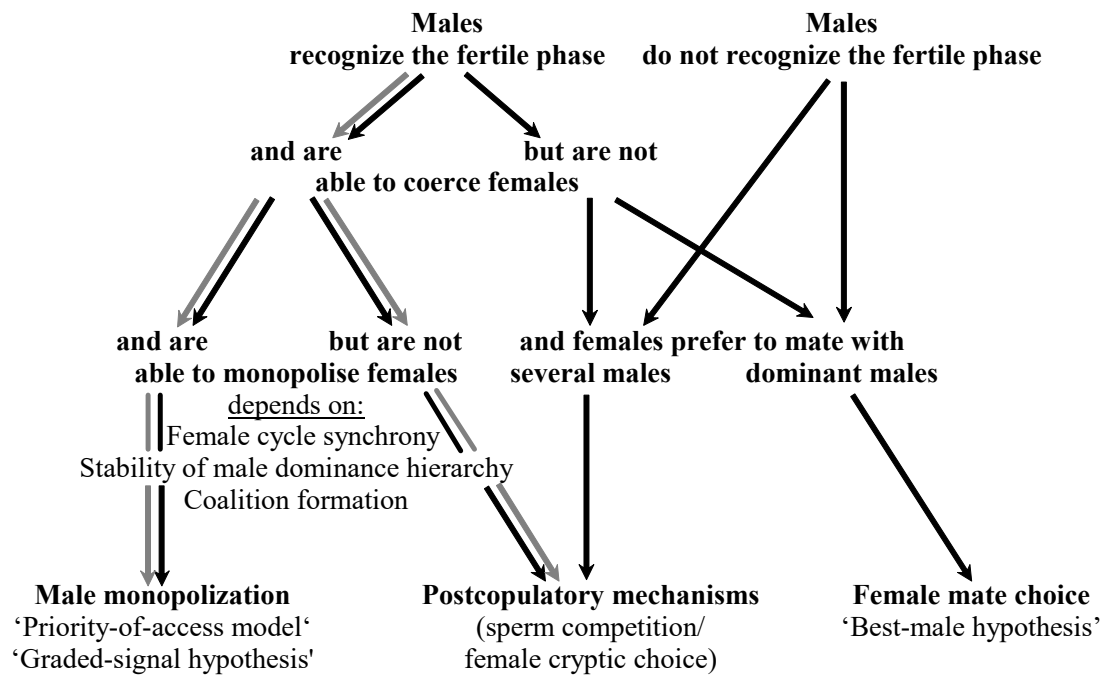
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Fig. 5



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Fig. 6