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Mate guarding and paternity in mandrills: factors influencing alpha male monopoly

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We used long-term data on mate guarding and paternity in mandrills, *Mandrillus sphinx*, (1) to examine cycle day and cycle selection by males; (2) to examine associations between male rank, periovulatory mate guarding and paternity outcome; (3) to test the predictions of the priority-of-access model; and (4) to investigate factors influencing the ability of alpha males to monopolize females. Males mate-guarded on periovulatory days more than on other receptive days, and during conceptive cycles more than during nonconceptive cycles. Both periovulatory mate guarding and paternity outcome correlated significantly with male rank. Alpha males accounted for 94% of periovulatory mate guarding and 69% of paternity, confirming the existence of extremely high reproductive skew in this highly sexually dimorphic species. The fit of the observed distributions of mate guarding and paternity to predictions from the priority-of-access model was good, but in both cases the alpha males accounted for a greater proportion of reproduction than predicted. Mate guarding was a good predictor of paternity, but consistently overestimated the reproductive success of the alpha male. Splitting data into group-years revealed that the percentage of mate guarding by the alpha male decreased with increasing numbers of adult males, and the percentage of paternity decreased with increasing numbers of reproductive males (all postpubertal males). Furthermore, mate guarding became less effective as the number of reproductive males increased. We attribute this to the fact that only males aged 8 years or more mate-guarded, but that all males aged at least 3.8 years may sneak copulations, reducing the effectiveness of mate guarding and therefore reducing paternity concentration in the alpha male.

Where receptive females are aggregated in space, males can potentially defend access to them, favouring large, strong, competitive males that are capable of excluding less competitive rivals from mating (Darwin 1871). Thus, reproduction is expected to be skewed towards socially dominant males. In a review of the influence of dominance rank on a variety of measures of reproductive success, Ellis (1995) showed that, with the exception of primates, the available evidence upheld the hypothesis that dominant males should obtain greater reproductive success than do subordinate males. However, Ellis (1995, page 259) highlighted the fact that 'most of the controversy surrounding whether or not dominance and RS [reproductive success] are positively related is confined to primates'. Indeed, the influence of dominance rank on male reproductive success has long been a central issue in primate sociobiology (Zuckerman 1932; Carpenter 1942; Altmann 1962), and has been the source of a great deal of debate (Bercovitch 1991, 1992; Cowlishaw & Dunbar 1991; Bulger 1993; Alberts et al. 2003; van Noordwijk & van Schaik 2004). In general, high-ranking males do sire more offspring than low-ranking males. However, variation in the relation between dominance rank and male reproductive success has been demonstrated at the species, population and group level, and at the temporal level within the same group (reviewed in van Noordwijk & van Schaik 2004).

The strength of the relations between male rank, mating success and paternity, and the resulting degree

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of reproductive skew in favour of alpha males, can be expected to depend on a number of factors that influence the ability of high-ranking males to monopolize access to receptive females. These include the number of females available and the temporal distribution of female receptivity (Emlen & Oring 1977; Ims 1989; Shuster & Wade 2003), the number of rival males present and the success of alternative mating strategies by subordinate males, male mate choice where females differ in quality or likelihood of conception, female reproductive strategies including mate choice (Bercovitch 1991; Alberts et al. 2003) and strategies to increase the number of males with which females mate (Hrdy 1979; van Schaik et al. 2004), and interactions between male and female strategies (e.g. Soltis et al. 2001).

Large female cohorts increase the chances of females cycling synchronously, posing a problem for the top-ranking male. In such cases, the priority-of-access model predicts that dominance rank should function as a queue for mating opportunities (Altmann 1962; Suarez & Ackerman 1971; Hausfater 1975). Males of any given rank are not expected to mate-guard unless all higher-ranking males are already mate guarding. Where females are asynchronously receptive, the top-ranking male should monopolize reproduction, but where more than one female is simultaneously receptive males of lower ranks are also expected to mate-guard. Variability in male mating and reproductive success should thus directly reflect male dominance status and the number of simultaneously oestrous females (Altmann et al. 1996).

Even when female receptive periods are asynchronous, an increased number of receptive females may reduce alpha male monopoly of receptive females, as the costs associated with mate guarding (risks of conflict with rival males and constraints on foraging, Bercovitch 1983; Alberts et al. 1996) may render an alpha male unable to guard successive females continuously, or almost continuously, over long periods. For example male chacma baboons, *Papio hamadryas ursinus*, mate-guard for only 9–12 days per month, regardless of the availability of periovulatory females, and leave some periovulatory females unguarded, implying that males are able to afford the costs of mate guarding for a limited period only (Weingrill et al. 2003).

Increased numbers of males (residents and extragroup males) are predicted to reduce monopoly of receptive females by high-ranking males for three reasons. First, increased numbers of rival males imply that more subordinate males are available to use alternative strategies, including surreptitious matings (Setchell, in press) that act to reduce the effectiveness of mate guarding, and more potential partners are available for coalition formation to displace mate-guarding males (Bercovitch 1988; Noë & Sluijter 1990; Watts 1998). Second, the presence of many males may result in decreased power differentials between individual males, making it more difficult for the alpha male to monopolize females. Even males with high resource-holding potential may be 'swamped', and unable to resist repeated challenges from multiple rivals (Cowlishaw & Dunbar 1991). Finally, the presence of more rivals may also make the male dominance hierarchy less stable, and rank instability itself may also weaken the relation between male rank and reproductive success (Cowlishaw & Dunbar 1991).

Finally, models of dominance-based priority of access to receptive females assume that all female cycles are equal. However, this is unlikely to be the case, and males may be expected to apportion costly mating effort in relation to the quality of an individual female and cycle. In particular, males are expected to mate-guard on days when females are most likely to be fertile, in preference to other days, and should mate-guard during conceptive cycles in preference to nonconceptive cycles, if they are able to distinguish between the two (e.g. Bulger 1993; Weingrill et al. 2003).

Owing to the difficulty of collecting long-term data for long-lived, slow-reproducing species, few studies have examined temporal variation in the extent to which male rank predicts male reproductive success in primates (but see Alberts et al. 2003; Widdig et al. 2004). The predictions of the priority-of-access model have been tested in detail only for baboons (Hausfater 1975; Noë & Sluijter 1990; Bulger 1993; Altmann et al. 1996; Weingrill et al. 2000; Alberts et al. 2003), although Soltis et al. (2001) have shown that the number of females mating simultaneously is associated with the strength of the correlation between male dominance rank and reproductive success in Japanese macaques, *Macaca fuscata*, and breeding seasonality (an estimator of female cycle synchrony) is known to influence the association between male rank and reproductive success (Paul 1997; van Noordwijk & van Schaik 2004). Tests of the priority-of-access model in baboons have revealed interesting subspecies differences. In chacma baboons, male mating success shows a very close fit to a dominance-based priority-of-access model (Bulger 1993; Weingrill et al. 2000). In yellow baboons, *P. h. cynocephalus*, however, although the correlation between observed mating behaviour and paternity and that expected from the priority-of-access model can be high (Altmann et al. 1996), the quantitative fit to the priority-of-access model is generally poor (Alberts et al. 2003). Alberts et al. (2003) attributed these subspecies differences to the expression of male–male coalitionary behaviour in yellow baboons, a behaviour that has not been observed for chacma baboons.

In this study we investigated the relations between male rank, mating success and paternity outcome in a semifree-ranging colony of mandrills, *Mandrillus sphinx*, using 13 group-years of behavioural observations and 10 group-years of paternity results. Mandrills were formerly thought to be close relatives of *Papio* baboons, but are in fact more closely related to *Cercocebus* mangabeys (Disotell et al. 1992; Fleagle & McGraw 1999). They are one of the most sexually dimorphic primate species, suggesting that male–male competition for access to periovulatory females is intense. Adult males (31 kg) are 3.4 times the mass of females (Setchell et al. 2001), have upper canines measuring 44 mm (Setchell & Dixson 2002), and possess showy secondary sexual ornamentation, including brightly coloured skin on the face, rump and genitalia.

Mandrills are found only in the dense rainforest of central Africa (Gabon, Republic of Congo, Equatorial

Guinea and Cameroon, Grubb 1973), and have so far proved impossible to habituate in the wild. Most of our knowledge of reproduction in this species therefore comes from a semifree-ranging colony of animals at the Centre International de Recherches Médicales, Franceville (CIRMF), Gabon. Studies of this colony show that multiple males associate with the social group of females and their young (Wickings et al. 1993; Setchell & Dixson 2001a), and observations from the wild confirm this multimale, multifemale social system (Abernethy et al. 2002). Breeding is moderately seasonal, with the majority of female receptive periods occurring between June and October (Setchell & Wickings 2004).

DNA analyses have shown that the alpha male mandrill sires the majority of offspring in a mating season (Dixson et al. 1993; Wickings et al. 1993; Wickings 1995; Charpentier et al. 2005). However, the only available behavioural data regarding reproduction concern 12 conceptive cycles during a single mating season (Dixson et al. 1993; Wickings et al. 1993). Like chacma baboons, male mandrills do not form coalitions (Setchell & Wickings 2005), predicting that mandrills should fit the priority-of-access model. If, however, lower-ranking males still manage to sire more infants than expected, then sneak copulations are the most likely explanation, in view of the dense forest habitat.

Our objectives were (1) to examine patterns of mate guarding by cycle day, as this is the first detailed study of mate guarding in mandrills, and to compare conceptive and nonconceptive cycles; (2) to examine the relations between male rank, periovulatory mate guarding and paternity outcome; (3) to examine specifically the predictions of the priority-of-access model; (4) to investigate variation in alpha male monopoly of mating and reproduction, and inconsistencies between mate guarding and paternity outcome, in relation to numbers of receptive females, numbers of adult and reproductive males, and alpha male tenure.

METHODS

Study Animals

The CIRMF mandrill colony was established in 1983–1984 when 15 animals (seven males, eight females) were released into a 6.5-ha forest enclosure (E1). There have been no subsequent additions to the colony, other than by breeding, although animals have occasionally been removed, and in 1994 a second semifree-ranging group was established in a smaller enclosure (E2, 3.5 ha) by transferring 17 mandrills (including six adult females and four adult males) from the first enclosure. The animals forage freely and receive daily supplements of monkey chow, fruit and vegetables. Water is always available from a stream, which runs through both enclosures. Behavioural observations are made twice daily (at ca. 1000–1130 hours and 1530–1730 hours) from a tower overlooking the enclosures. This study makes use of records of female cycle status and male mate guarding for E1 and E2 for the 8-year period 1996–2003. The size and age–sex composition of the study groups during this period (Table 1) correspond to those of the smaller groups observed in the wild (Rogers et al. 1996). The research was approved by CIRMF and the Comite Regional d'Ethique Ile de France Sud.

All males above the age of 3.8 years, the age at which the testes descend (Setchell & Dixson 2002), were considered potentially reproductive. However, males do not attain adult body mass, crown–rump length or full expression of secondary sexual traits until 10 years (Setchell & Dixson 2002). Males aged 3.8–8.0 years

Table 1. Composition of the study groups, with numbers of cycles, conceptions and known paternities

Year	Adult males*	Older adolescent males†	Younger adolescent males‡	Reproductive females§	Juveniles and infants	Total group size	Number of cycles	Number of conceptions	Number of known paternities
Enclosure 1									
1996	1	4	6	13	12	36	18	12	11
1997	3	5	6	13	20	47	15	9	5
1998	5	4	8	19	29	65	14	13	11
2000	8	1	12	22	24	69	18	18	15
2001	6	3	12	27	28	81	19	11	9
2002	8	3	14	31	48	104	25	10	0
2003	5	2	7	19	36	69	18	8	0
Enclosure 2									
1996	5	0	4	6	6	21	9	7	6
1997	4	2	2	6	14	28	2	1	1
1998	4	2	3	10	11	30	5	7	7
2000	4	0	5	13	14	36	8	9	6
2001	4	0	6	13	21	44	5	4	3
2002	4	2	5	15	26	52	14	11	0
2003	3	3	6	16	14	42	4	4	0

*Males >10 years, based on age on 1 May, the approximate beginning of the mating period.

†Males 8–10 years.

‡Males 3.8–8.0 years.

§Females undergoing reproductive cycles.

(sexually mature, but small) were termed young adolescent males, males aged 8.0–10.0 years (sexually mature, approaching adult size and appearance) were termed older adolescent males, and males aged 10.0 years and older (full size) were termed adult males. Females were termed reproductive once they had shown their first full swelling cycle (see below), nulliparous when they had not yet given birth to an infant, and parous when they had already given birth.

Female Cycle Status

Female mandrills show sexual swellings that increase in size during the follicular phase, reaching maximum size around the time of ovulation. No endocrine data are yet available for mandrills, but studies of closely related baboons have shown that the sexual swelling grows larger at the same time as oestrogen levels increase during the follicular phase of the menstrual cycle; a rapid decrease in sexual swelling size (break-down) coincides with a postovulatory rise in progesterone; and the swelling detumesces during the luteal phase until it is flat (Wildt et al. 1977; Shaikh et al. 1982). Cycle days were numbered according to the day of deflation, with the day of break-down termed day 0, and preceding days assigned negative numbers (following Hausfater 1975). We restricted analyses of male mating success to the 6 days before swelling break-down, termed the 'periovulatory period'. This encompasses the period during which ovulation and conception are most likely to occur (Hendrickx & Kraemer 1969; Wildt et al. 1977; Shaikh et al. 1982). Cycles were termed conceptive when they preceded the appearance of a pregnancy swelling. All such cycles during the study period resulted in the birth of a live, full-term infant.

Mate Guarding

Systematic, focal observations of sexually receptive females are not possible under colony conditions. We therefore used the occurrence of mate guarding as a behavioural estimate of male attempts to secure unique access to a receptive female. This is an easily observed, unambiguous behaviour, where a male maintains close proximity to a female, and monitors her continuously, and has commonly been used as a measure of mating success in baboons (Smuts 1985; Bercovitch 1986; Noë & Sluijter 1990; Bulger 1993; Altmann et al. 1996; Weingrill et al. 2000; Alberts et al. 2003).

Daily records were kept of the occurrence of mate guarding, with the identity of the male and female involved, and the reproductive status of the female. Mate-guarding dyads were not observed to change between morning and afternoon observation sessions. This observation was reinforced by ad libitum observations at other times, which also suggested that mate-guarding males remained close to the females at night, although darkness presumably increases the chances of sneak copulations. We therefore assumed that mate guarding continued outside observation periods. Cycles for which observations were available for fewer than 4 of the 6 periovulatory days were discarded from behavioural analyses. Observations were available for 4 or more periovulatory days for 171 female cycles, from 44 females ($\overline{X} \pm \mathrm{SEM} = 3.9 \pm 0.5$ cycles per female, range 1–16, distribution across the years of the study is shown in Table 1).

Dominance Hierarchies

We determined rank relations between males from ad libitum records of avoidance behaviour during daily observation periods. With the exception of occasional dramatic changes in male rank that occurred from one day to the next and usually involved a change in alpha male (see Results), all adult and older adolescent males could be assigned a rank for each mating season, although data were not always available for younger adolescent males. We should note that our focus on the influence of male rank means that the same male may contribute to data for multiple ranks over the study period.

Paternity Determination

We determined paternities for 74 of the 91 offspring (81%) born following mating seasons in 1996–2001 (insufficient or no blood samples were available for the remaining 17 individuals). Table 1 shows the distribution of known paternities by group and mating season. Details of paternity determination can be found in Charpentier et al. (2005). Briefly, DNA was extracted from blood samples obtained during annual captures. Maternity was verified and paternity assigned using 8–10 microsatellite loci. Genotypes were available for all potential sires (all reproductive males present at the time of conception), and paternity was assigned using CERVUS 2.0 (http://helios.bto.ed.ac.uk/evolgen/cervus). CERVUS 2.0 is based on the likelihood-based approach described in Marshall et al. (1998). Simulations were carried out to estimate the critical difference in log likelihood score between the most likely and the second most likely candidate father. Simulation input parameters were 2.4% rate of typing errors, 92.6% of loci typed and 10 000 cycles, with 100% of candidate males genotyped. In 65 cases CERVUS assigned a sire with a 95% confidence level, and for a further nine cases CERVUS sires were attributed at only a relaxed level (80%). In the latter cases, we used PARENTE (Cercueil et al. 2002) to confirm the sire. This software uses a Bayesian method to calculate the probability of paternity for each sire using information from all possible sires in the population. For each individual, PARENTE verifies the genetic and age compatibilities for all potential triads (individual, potential mother, potential father), and calculates the probability that a parentage link is correct using the allelic frequencies and the sampling rate of the population, taking into account incompatibilities and the error rate (estimates of the error rate in the data and mean proportion of loci typed were the same as for CERVUS).

Data Analysis

We analysed periovulatory mate guarding (1) with data for all cycles for which data were available, (2) with data for conceptive cycles only, and (3) separately for each of the 13 group-years for which data were available (1996–2003, no data for either enclosure in 1999, none for E2 in 2001). Mating success for each individual male was defined as the number of periovulatory days that he mate-guarded. Mating success for each male rank was defined as the number of periovulatory days on which a male of that rank was observed to mate-guard.

We analysed reproductive success for 1996–2001, and separately for each of the 10 group-years for which data were available (1996–2001, no data for either enclosure in 1999 because no females conceived). Reproductive success for each individual male was defined as the number of offspring sired, and reproductive success for each male rank was defined as the number of offspring sired by a male of that rank.

Factors influencing alpha male monopoly

To investigate the ability of the alpha male to monopolize receptive females, we used the percentage of all periovulatory mate guarding by the alpha male for each group-year. All cycles (conceptive and nonconceptive) were used in this analysis, as we could not assume that nonconceptive cycles were nonfertile. To investigate the ability of the alpha male to monopolize reproduction, we used the percentage of offspring of known paternity that he sired. We chose to examine percentage monopoly by the alpha male (similar to the 'paternity concentration' variable used by van Noordwijk & van Schaik 2004), rather than the correlation coefficient between male rank and reproductive success (e.g. Cowlishaw & Dunbar 1991), owing to the high numbers of nonsires in each year, the small cohorts of reproductive males in some years, and the problematic influence of younger adolescent males on correlation coefficients (Bercovitch 1986; McMillan 1989).

Predictions of the priority-of-access model

The priority-of-access model predicts that lower-ranking males should mate-guard females only on days when more than one female is simultaneously periovulatory. The expected distribution of mate guarding among males was therefore calculated from the observed overlap of female periovulatory periods during the study period as follows: the expected proportion of mate guarding by the alpha male equalled the number of days that one or more female was periovulatory, divided by the total number of female days; the expected proportion of mate guarding by the second male equalled the number of days that two or more females were periovulatory, divided by the total number of female days; and so on for lower-ranking males. We used both conceptive and nonconceptive periovulatory periods in this analysis, as we had no way of knowing whether nonconceptive cycles were fertile or not.

To calculate priority-of-access predictions for paternity we used only conceptive periovulatory periods for which the sire of the resulting offspring was known, and based our calculations on the maximum number of females overlapping on any one day of the periovulatory period concerned. Thus, where no other female was simultaneously periovulatory, the alpha male was awarded the offspring. Where one other female was simultaneously periovulatory, the alpha was awarded half an offspring, and the second-ranking male half an offspring. Where two other periovulatory females were also available on any one day of the periovulatory period, the alpha was awarded a third of an offspring, the second-ranking male a third of an offspring, and the third male a third of an offspring, etc. These predictions are conservative, as they assume that a female is equally likely to conceive on each of the 6 days of the periovulatory period. If, in reality, males can determine likelihood of ovulation more precisely, then they will not need to mate-guard all 6 days of the periovulatory period.

Deviation from the priority-of-access model

To examine factors influencing the fit of the priority-of-access model to the observed data, we calculated the deviation of the observed proportion of all mate guarding attributed to the alpha male from the expected proportion of all mate guarding by the alpha male for each group-year as the percentage observed less the percentage expected, divided by the percentage expected, using expected values calculated from the priority-of-access model. A similar variable was calculated for deviation of observed paternity from the priority-of-access model.

Potential influences on alpha male monopoly

To determine the best predictor(s) of the extent of alpha male monopoly of mate guarding and paternity, the number of males siring per year, deviation from the priority-of-access model for mate guarding and paternity, and the discrepancy between alpha male mate guarding and paternity, we used stepwise multiple linear regression with a forward selection procedure, and the following independent variables: numbers of receptive females, adult males and reproductive males (adults and adolescents) present in the group, and the tenure of the alpha male (P to enter $= 0.05$, P to remove $= 0.10$). All variables were normally distributed (skew/standard error of skew <3, Zar 1996). Although variables that contribute to total group size (numbers of receptive females, adult males and reproductive males) are clearly related, in no case was tolerance less than 0.336 (variance inflation factor > 2.97), meaning that collinearity was not a serious problem in these analyses (Quinn & Keough 2002 proposed tolerance <0.1, or VIF > 10.0, as an approximate guide to unacceptable collinearity).

For all statistical analyses we used SPSS 11.0 (SPSS Inc., Chicago, IL, U.S.A.). Means are quoted ±SEM. All tests were two tailed.

RESULTS

Male Dominance

Patterns of male avoidance revealed that there was always one top-ranking male (alpha male) in a group. All other males avoided this individual, who never avoided other males. Of a total of 20 males (12 in E1, 8 in E2) that were already adult at the beginning of the study, or who reached adulthood during the study period, nine attained top rank (seven in E1, two in E2). Males attained top rank at ages 8.8–12.6 years (mean 10.8 ± 0.6 years), and lost top rank at 10.5–19.0 years (mean 13.8 ± 1.3 years).

Six changes in alpha male occurred in E1 during the 8-year study. All five of these that occurred naturally (i.e. were not as a result of human intervention) occurred when at least one, and up to 10, females showed sexual swellings. In three of the four cases where details of the take-over were known, two or more females were periovulatory. Mean male tenure in this enclosure was 1.6 ± 0.5 years (range 0.2–3.5 years). By contrast, only one change in alpha male occurred in E2 during the study. One female showed a sexual swelling at the time of the take-over, but none were periovulatory. The tenures of the two alpha males in this enclosure were 2.4 years (estimated date of take-over) and a minimum of 7.5 years (ongoing at the end of the study), respectively. Differences in group size may help to explain the difference in alpha male turnover and tenure between the two enclosures. First, E1 contained significantly more reproductive females per year across the study period than E2 (paired Student's *t* test: $t_{12} = 3.12$, $P = 0.009$; Table 1). Second, fewer males matured and reached adulthood in E2 (four maturing males, mean 0.6 ± 0.6 per year) than in E1 (11 maturing males, mean 1.4 ± 1.0 per year), although this difference was not significant ($t_{12} = 0.81$, $P = 0.096$).

Mate Guarding

Cycle day selectivity

Timing of mate guarding relative to day of break-down was similar for both conceptive and nonconceptive cycles (Fig. 1). Mate guarding never occurred earlier than day −25 (although females could show sexual swellings from up to day −40), after the day of break-down, or during pregnancy. Mate guarding increased gradually from day −24, remaining less than 20% until day −10. It was highest during the presumed periovulatory period (days −6 to −1), peaking on day −4 (conceptive cycles) and day −3 (nonconceptive cycles), and decreasing abruptly to less than 1% on the day of break-down. The maximum percentage of females mate-guarded on any one cycle day was 57% (conceptive cycles) or 51% (nonconceptive cycles). Mate guarding during conceptive cycles was systematically higher than during nonconceptive cycles after day −19 (paired *t* test for days −20 onwards: $t_{20} = 4.89$, $P < 0.001$).

Alpha males mate-guarded with the highest frequency on all cycle days for both conceptive and nonconceptive cycles, whereas nonalpha males never mate-guarded more than 5% of days observed for any cycle day (mean 1.6 ± 0.3%, day −20 to break-down). The marked increase in mate guarding towards and during the periovulatory period was thus due almost entirely to increased mate guarding by the alpha male. Plotting mate guarding versus days since swelling onset revealed no marked peak in male sexual activity (Fig. 1).

Cycle selectivity

Where alpha males (who had 'free' choice) had the choice of two females, one of which conceived and the other did not, they were significantly more likely to mate-guard the female that conceived ($N = 34$) than the female that did not conceive ($N = 11$; $\chi^2_1 = 11.76$, $P < 0.001$). Where three periovulatory females were available simultaneously, but only one of the three conceived, the alpha male mate-guarded the female that conceived on 10 occasions, and mate-guarded one of the other two females on eight occasions. This was significantly different from random choice, which predicts that the male should guard the female that conceived on a third of days ($\chi^2_1 = 4.00$, $P = 0.046$). Finally, where two of the three available females conceived ($N = 10$ cases), the alpha male mate-guarded one of these two females on nine occasions, and the female that did not conceive on only one occasion, although this was not significantly different from random choice ($\chi^2_1 = 0.245$, $P = 0.118$).

Who mate-guarded?

Most female cycles were mate-guarded by only one male, with a maximum of three males mate guarding during any one cycle or periovulatory period, and a maximum of two males mate guarding during any conceptive periovulatory period (Fig. 2). Seventeen males mate-guarded at least once during the study period, but only 11 of these mate-guarded during a conceptive periovulatory period. Mate-guarding males were aged 8.3–18.8 years, with a mean age of 12.8 ± 0.5 years (using one age-point for each mate-guarding male per mating season). Variance in total days mate-guarded was high among males that mate-guarded at least once. The most successful male in E1 accounted for 33% of all conceptive periovulatory mate guarding, whereas the most successful male in E2 accounted for 83%, a difference related to the difference in alpha male tenure in the two groups. The individual contribution of mate-guarding males ranged from 1 to 121 conceptive cycle days (mean 29 ± 10 days), 0 to 48 nonconceptive cycle days (mean 13 ± 4 days), 0 to 83 conceptive periovulatory days (18 ± 6 days) and 0 to 40 nonconceptive periovulatory days (9 ± 3 days). Of the 26 males that attained the age of 8 years before or during the study period, nine (35%) were never observed to mate-guard.

Continuous mate guarding

The distribution of female cycles was such that alpha males often mate-guarded one female immediately after another. Unbroken data (with no missing days) were available only for portions of the study period, limiting investigation of continuous mate guarding. However, data from the most complete years (1996 and 1997) showed

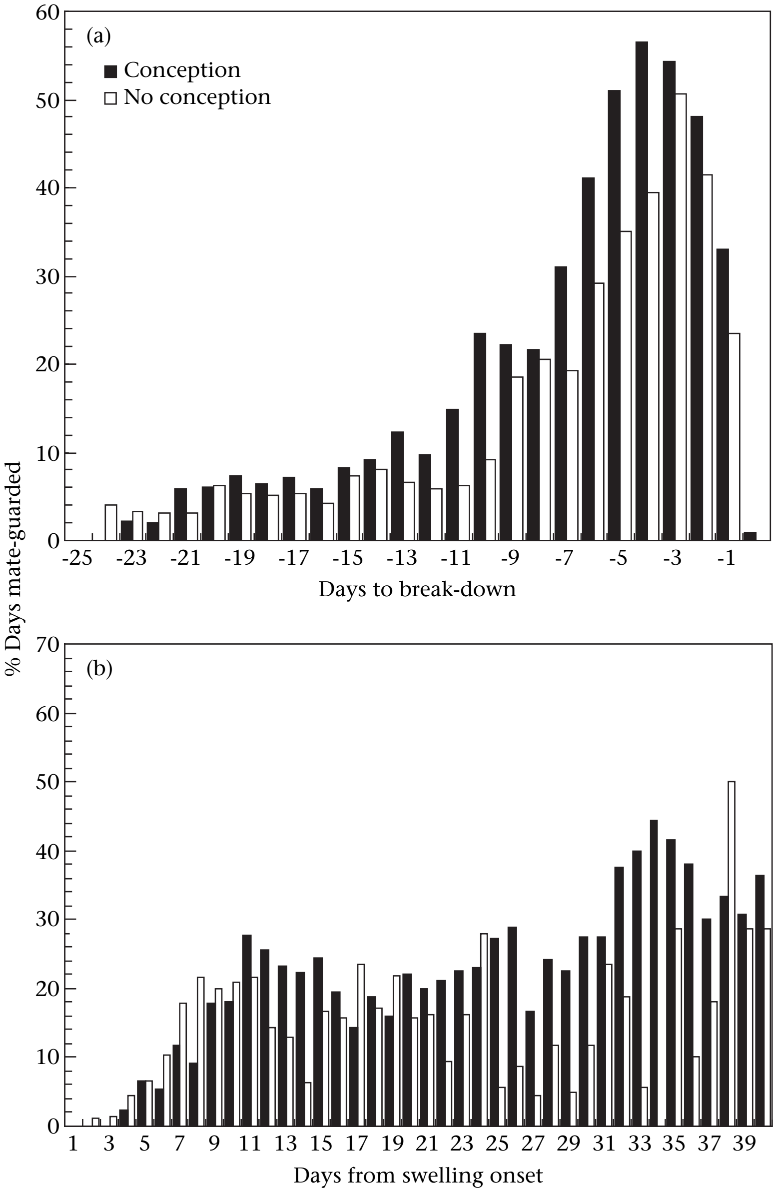

Figure 1. Percentage of conceptive and nonconceptive cycles on which mate guarding occurred versus (a) number of days to sexual swelling break-down and (b) days since onset of sexual swelling. $N = 27$–106 for conceptive cycle days (mean ± SEM = 72 ± 4), and 18–92 for nonconceptive cycle days (53 ± 4).

that alpha males mate-guarded individual females continuously for a mean of 5.3 ± 5.4 days, and the alpha male could mate-guard continuously for up to 22 days (with the same or multiple females), and for much longer periods with only 1–3 days without mate guarding (e.g. 58 days in 1996).

Male dominance rank and mate guarding

Males ranked 1–3 mate-guarded during conceptive periovulatory periods, whereas males ranked 1–4 mate-guarded during nonconceptive periovulatory periods. Males ranked 1–6 mate-guarded on other cycle days (conceptive and nonconceptive), but males ranked 6+ never mate-guarded. Alpha males accounted for over 90% of mate guarding and where a change in alpha male occurred, the new alpha male took over mate guarding on the same day that he took over top rank.

The number of periovulatory days (conceptive and nonconceptive) mate-guarded and male rank were highly and significantly correlated (pooling males ranked 6+ because they did not mate-guard: $r_S = -0.899$, $N = 6$, $P = 0.015$, the correlation is negative because the top-ranked male ranks 1, Fig. 3), and this remained the case when the alpha male was removed from analysis ($r_S = -0.900$, $N = 5$, $P = 0.037$). The number of males available to mate-guard (i.e. those aged 8+ years) during a mating season ranged from 4 to 11, and potentially mate-guarding males ranked 5 and 6 were not available for 2 of the 13 group-years. However, correcting the proportion of mate guarding due to each rank for opportunity (the number of periovulatory days available to males of

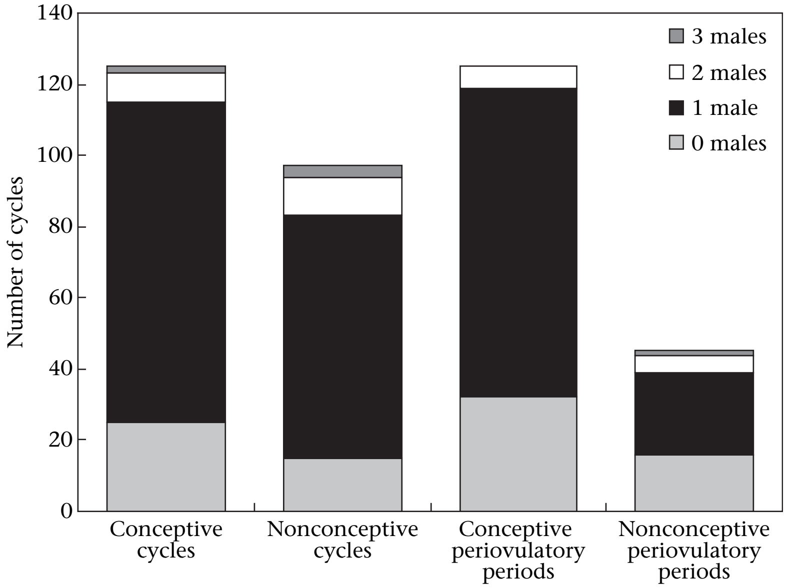

Figure 2. Number of males that mate-guarded females during each conceptive and nonconceptive cycle, and during each conceptive and nonconceptive periovulatory period.

that rank aged 8+ years and therefore available to mate-guard) only increased the strength of the correlation between dominance rank and periovulatory days mate-guarded ($r_S = -0.943$, $N = 6$, $P = 0.005$).

When we considered only mate guarding during conceptive periovulatory periods, alpha males accounted for 94% of mate guarding (258/275 days), second-ranking males 2% (6 days) and third-ranking males 4% (11 days). Here, the correlation with rank, pooling all ranks that did not mate-guard, was nonsignificant ($r_S = 0.400$, $N = 4$, $P = 0.600$). However, including all males aged 8+ years (i.e. males available to mate-guard) resulted in a significant negative correlation with male rank ($r_S = -0.880$, $N = 6$, $P = 0.021$). As there were always more than three males aged 8+ years present, it was not necessary to adjust these figures for opportunity.

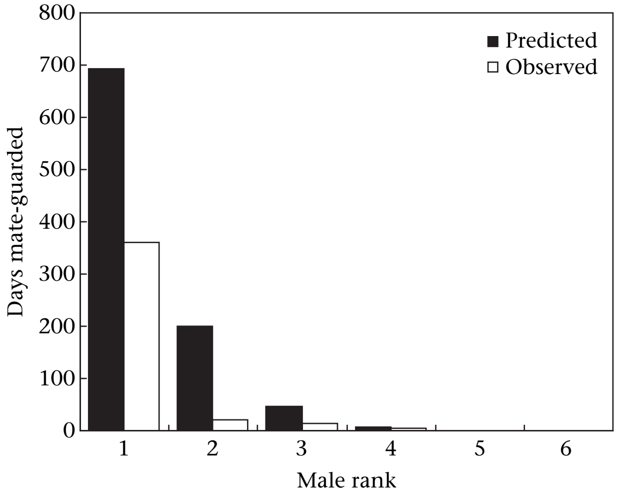

Figure 3. Number of periovulatory days mate-guarded by males of each rank. Predicted values were calculated from the distribution of female periovulatory periods, using the priority-of-access model.

Factors influencing alpha male monopoly

The alpha male accounted for 77–100% of periovulatory mate guarding (mean 94 ± 2%) in any one group-year, and was the only male to mate-guard periovulatory females for 7 of 13 group-years. The number of males that mate-guarded during any one group-year ranged from 1 to 4 (mean 2.0 ± 0.3), representing 11–80% (mean 32 ± 6%) of the males aged 8+ years available to mate-guard. The only significant predictor of alpha male monopoly of mate guarding was the number of adult males present, whereas the number of reproductive males, number of receptive females and alpha male tenure were excluded from the model (Table 2). The alpha male monopolized all mate guarding until there were more than three adult males present, and was capable of doing so until more than five adult males were present.

Mate guarding and the priority-of-access model

Although up to 16 females could show sexual swellings on any one day, a maximum of six were simultaneously periovulatory, and on 65% of periovulatory days no other female was periovulatory (Fig. 4). There were more adult males present than there were periovulatory females for all but 12 of 889 periovulatory days (1%), and there were always more males aged 8+ years available than periovulatory females (i.e. the operational sex ratio was always male biased). However, only one male mate-guarded on 381 of 403 mate-guarded periovulatory days (95%), and a maximum of two males mate-guarded on any one periovulatory day (22 days).

Figure 3 includes the predicted proportion of mate guarding for males of each rank, calculated using the priority-of-access model, for all periovulatory days for which mate-guarding information was available. The predicted number of mate-guarding days is greater than the observed figures, because mate guarding occurred on only

Table 2. Results of multiple regressions investigating the influence of various predictor variables on monopoly of mate guarding and paternity by alpha males

		Mean square							
Dependent variable	R^2_{adj}	Regression (*df*)	Residual (*df*)	*F*	*P*	Predictor variables	β	*t*	*P*
Alpha male monopoly of mate guarding	0.403	353.92 (1)	427.31 (11)	9.111	0.012	No. of adult males	−0.673	−3.018	**0.012**
						No. of reproductive males	0.143	0.417	0.686
						No. of receptive females	0.069	0.239	0.816
						Alpha male tenure	−0.213	−0.826	0.428
Deviation of mate guarding from priority-of-access model	0.271	0.098 (1)	0.197 (11)	5.470	0.039	No. of adult males	−0.411	−1.405	0.190
						No. of reproductive males	0.090	0.213	0.835
						No. of receptive females	0.576	2.340	**0.039**
						Alpha male tenure	−0.148	−0.535	0.604
Alpha male monopoly of paternity	0.406	2227.525 (1)	344.354 (8)	6.469	0.038	No. of adult males	0.106	0.041	0.969
						No. of reproductive males	−0.693	−2.543	**0.038**
						No. of receptive females	0.318	0.648	0.541
						Alpha male tenure	−0.247	−0.727	0.494
Number of males siring	0.674	13.416 (1)	0.685 (8)	19.573	0.002	No. of adult males	−0.125	−0.473	0.650
						No. of reproductive males	0.843	4.424	**0.002**
						No. of receptive females	−0.125	−0.473	0.650
						Alpha male tenure	−0.203	−0.909	0.394
Discrepancy between mate guarding and paternity	0.546	1536.542 (1)	1299.822 (8)	11.836	0.009	No. of adult males	−0.471	−1.808	0.114
						No. of reproductive males	0.772	3.440	**0.009**
						No. of receptive females	−0.194	−0.489	0.640
						Alpha male tenure	−0.204	−0.763	0.470

Significant *P* values are highlighted in bold for predictor variables.

403 of 948 (43%) of available periovulatory days (see also Fig. 1). The qualitative match between the observed and predicted distributions of mate guarding by rank was good, but not perfect, and deviation from the model was significant ($\chi^2_3 = 28.47$, $P < 0.001$). This was due to the alpha male mate guarding proportionally more than expected (observed 90%, expected 73%), the second- and third-ranking males mate guarding proportionally less than expected (rank 2: observed 5%, expected 21%; rank 3: observed 3%, expected 5%), and males ranked 5 and 6 mate guarding, although they were not expected to do so.

Deviation from the priority-of-access model

The expected proportion of all mate guarding that was accounted for by the alpha male, predicted from the priority-of-access model, ranged from 63 to 100% across the 13 group-years, with a mean of 83 ± 3%. With one exception, where the alpha male mate-guarded less than expected, observed mate guarding by the alpha male was consistently higher than predicted (mean deviation from the expected value 0.15 ± 0.04, range −0.20–0.38). The only significant predictor of deviation from expected mate guarding was the number of receptive females present, whereas the number of adult males, number of reproductive males and alpha male tenure were excluded from the model (Table 2). As the number of receptive females increased, deviation from the priority-of-access model also increased (alpha males mate-guarded more than expected).

Paternity Outcome

Fourteen males sired offspring (10 in E1, four in E2) during the 10 group-years for which both paternity and mate-guarding data were available, although only six males mate-guarded conceptive periovulatory females during this period (four in E1, two in E2). Sires were aged 5.6–18.7 years, with a mean age of 11.4 ± 0.6 years ($N = 29$, using the age midpoint for each sire per mating season). Variance in number of offspring sired was high (E1: 1–13 offspring, mean 5.1 ± 1.4 offspring; E2: 1–18 offspring, mean 5.8 ± 4.1 offspring). The most successful male in E1 sired 25% of offspring, whereas the most successful male in E2 sired 78% of offspring in their respective groups (owing to differences in alpha male tenure between the two groups).

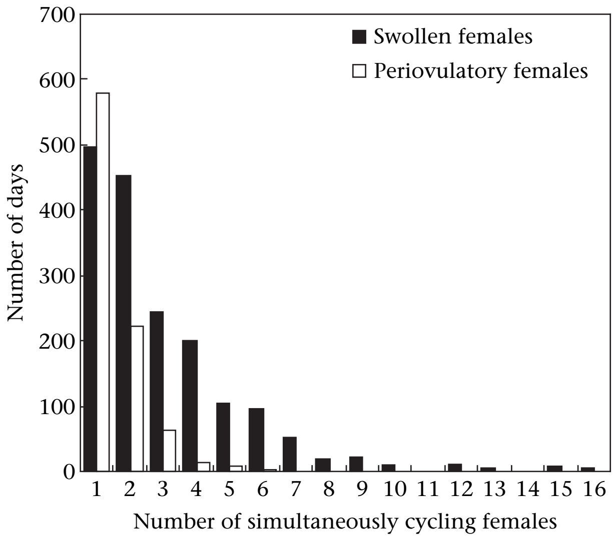

Figure 4. Number of sexually swollen and periovulatory females available on any one day during the study period.

Male dominance rank and paternity

Alpha males sired 51 of 74 offspring (69%), while the remaining 31% were sired by males ranked 2–10, with nonalpha males at each rank siring a maximum of five offspring (7%; Fig. 5). The mean rank of sires was 1.9 ± 0.2 (median 1, range 1–10) and the mean rank of the 23 nonalpha sires was 3.7 ± 0.5 (median 3, range 2–10). Contribution to paternity was significantly correlated with male dominance rank (pooling ranks greater than 10, $r_S = -0.837$, $N = 10$, $P = 0.003$). This was not only due to the influence of alpha males, as the correlation remained significant when they were removed from the analysis ($r_S = -0.760$, $N = 9$, $P = 0.018$). The number of offspring sired by males of each rank should be corrected for opportunity, as there were not always 10 potential sires available. However, a minimum of eight potential sires was always available (Table 1), and pooling ranks 8+ did not change the significance of the result ($r_S = -0.898$, $N = 8$, $P = 0.002$).

Factors influencing monopoly of paternity by the alpha male

Alpha males sired more offspring than any other male in all group-years. The percentage of paternity gained by the alpha male ranged from 33 to 100% (mean 74 ± 6%, 10 group-years), while one to five males sired offspring (mean 2.9 ± 0.5) representing 10–33% (mean 23 ± 3%) of reproductive males available. The only significant predictor of both percentage paternity by the alpha male and the number of males siring offspring was the number of reproductive males in the group, whereas the number of receptive females, number of adult males and alpha male tenure were excluded from both models (Table 2). As the number of reproductive males present increased, percentage paternity by the alpha male decreased, and the number of sires increased.

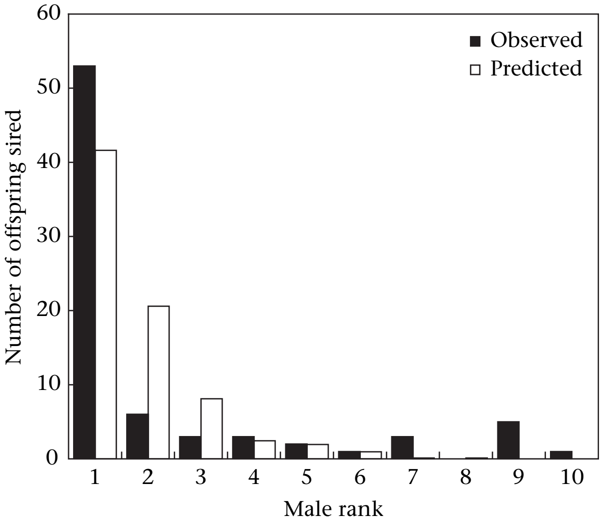

Figure 5. Number of offspring sired by males of each rank. Predicted values were calculated from the distribution of female periovulatory periods, using the priority-of-access model.

Paternity outcome and the priority-of-access model

Figure 5 includes predictions for paternity based on the priority-of-access model. The observed distribution of paternity was not significantly different to that predicted (pooling males ranked 4+, owing to low expected counts: $\chi^2_3 = 7.48$, $P = 0.058$). However, alpha males exceeded their predicted reproductive success by 1.2 times, whereas second- and third-ranking males sired fewer offspring than predicted (44% and 62% of offspring predicted, respectively). Notably, seventh- and 10th-ranking males were predicted not to sire at all, whereas they sired three offspring.

Deviation from the priority-of-access model

The value of the deviation from predictions of the priority-of-access model (whether the alpha sired more or fewer offspring than predicted) ranged from −0.20 to 0.63 (mean 0.11 ± 0.08, $N = 10$ group-years), and the alpha sired more offspring than predicted in 8 of 10 group-years. However, none of the variables tested (numbers of cycling females, adult males, reproductive males and alpha male tenure) significantly predicted this measure of deviation.

Mate guarding and paternity

At a general level, the number of offspring sired by a male was significantly positively correlated with both the number of days that he mate-guarded conceptive periovulatory females ($r_S = 0.636$, $N = 13$ sires, $P = 0.019$; Fig. 6), and the number of conceptive cycles that he mate-guarded ($r_S = 0.648$, $N = 13$, $P = 0.017$; both analyses based only on the period for which paternity data were available). This was also the case when only the six mate-guarding males were considered (number of days: $r_S = 0.812$, $P = 0.050$; number of cycles: $r_S = 0.928$, $P = 0.008$).

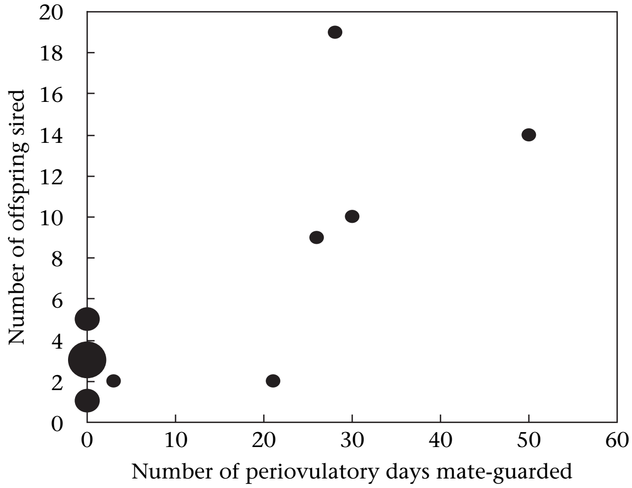

Figure 6. Number of conceptive periovulatory days mate-guarded versus number of offspring sired for the period for which both behavioural and paternity data were available. Small symbols indicate single data points, medium symbols indicate two data points, and large symbols indicate three data points.

At the level of individual offspring, of 57 infants where observations were available for the periovulatory period of the conceptive cycle the alpha male sired 37 (79%). The alpha male was significantly more likely to sire the resulting offspring if he mate-guarded during the periovulatory period than if he did not ($\chi^2_1 = 3.96$, $P = 0.046$). Furthermore, the alpha male mate-guarded more (median 50% of periovulatory days) when he sired the resulting offspring ($N = 37$) than when he did not (median 20%; $N = 20$; Mann–Whitney U test: $U = 254.00$, $Z = 1.96$, $P = 0.050$), although the range for both conditions was 0–100%, meaning that even where the alpha male mate-guarded during the entire periovulatory period, he was not necessarily the sire. In only one case (5%) did a non-alpha male both mate-guard and sire the resulting offspring. All males that mate-guarded sired offspring, but the six males that did not mate-guard sired 20 of 74 offspring (27%), indicating the success of surreptitious mating tactics.

Discrepancy between mate guarding and paternity

Although alpha males dominated both mate guarding and paternity, behavioural mating success overestimated reproductive success by the alpha male. The percentage of offspring sired by the alpha male in any one group-year was lower than the percentage of periovulatory mate guarding by the alpha male (Wilcoxon signed-ranks test: $T = 36$, $N = 10$ group-years, $P = 0.012$), and more males sired (1–5) than mate-guarded (1–3) during any one year ($T = 28$, $N = 10$, $P = 0.004$). The discrepancy between the percentage of mate guarding and the percentage paternity by the alpha male was 0–55% (mean 21 ± 5%). The only significant predictor of this discrepancy was the number of reproductive males present in a group, whereas the number of adult males, number of receptive females and alpha male tenure were excluded from the model (Table 2). As the number of reproductive males increased, the discrepancy between mate guarding and paternity by the alpha male also increased.

DISCUSSION

Our results confirm a robust relation between rank and reproduction in mandrills, with alpha males dominating both mate guarding and paternity. However, the strong control that alpha males exert over receptive females (in the form of mate guarding) does not necessarily translate into the proportion of offspring sired. This appears to be the result of alternative reproductive tactics by other males, in the form of sneak copulations, reducing the effectiveness of mate guarding. As the number of rival adult males increased, the proportion of mate guarding by the alpha male decreased. As the number of rival reproductive males (of all ages) increased, the proportion of paternity attributed to the alpha male decreased, the number of males siring increased, and the effectiveness of alpha male mate guarding decreased (the discrepancy between the percentage of mate guarding and the percentage paternity by the alpha male increased). As for male rhesus macaques (Widdig et al. 2004), yellow baboons (Alberts et al. 2003), blue monkeys, *Cercopithecus mitis* (Cords 2000), domestic cats, *Felis catus* (Say et al. 2001), and spotted hyaenas, *Crocuta crocuta* (Engh et al. 2002), these data for mandrills provide more support for limited or incomplete control models of reproductive skew, which predict that subordinates will reproduce when the capacity of dominant individuals to monopolize reproduction is reduced (Cant 1998; Clutton-Brock 1998; Reeve et al. 1998), than for concession models, which propose that dominant individuals have full control of reproduction, but allow subordinates to reproduce where such reproduction brings benefits to dominants, for example by enticing subordinates to remain and help defend the group (e.g. Vehrencamp 1983; Johnstone et al. 1999).

Monopolization of females, and consequent paternity concentration in the alpha male, leads to very high short-term variance in male reproductive skew. Whether this variance is maintained over a longer timescale depends on the length of alpha male tenure, and whether all males attain alpha status at some stage during their careers. Alpha males had shorter tenure when there were large numbers of maturing rivals and females. Similarly, Alberts et al. (2003) found that the tenure of alpha male yellow baboons was predicted most strongly by the number of adult males present, although the variance explained was low. Thus, larger groups reduce reproductive skew not only by reducing the ability of the alpha male to monopolize females, but also by reducing the tenure of alpha males, meaning that more males attain high status and reproductive success, but for shorter periods, and decreasing variance in male lifetime reproductive success. However, examination of male careers shows that not all males attain alpha status during their lifetime in this colony and variance in male lifetime reproductive output is high, and higher than in females, in agreement with the large body size, well-developed weaponry and late age at maturity in males compared with females (Setchell et al., in press).

Cycle Day and Cycle Selectivity

As reported for other primate species (reviewed by Dixson 1998), male mandrills showed clear preference for the periovulatory period of the female cycle. Our finding that males mate-guarded only 43% of periovulatory days is likely to be caused by the error associated with a 6-day periovulatory period estimate. If alpha males are able to predict the fertile period of a female more accurately than this 6-day window, then they need not necessarily mate-guard higher-ranking females on each day of their periovulatory period, but only on days when conception is likely. Cycle day selectivity was not related to the day of onset of sexual swelling, implying that the periovulatory period could not be predicted from the duration of sexual swelling. As suggested for other species with sexual swellings (e.g. Weingrill et al. 2003), it seems that male mandrills may rely on additional cues to determine timing of female ovulation, including olfactory (anogenital secretions) and tactile (swelling turgidity) cues, as well as visual inspection of swellings.

Males also appeared to be able to distinguish females that conceived from those that did not, mate guarding the former more than the latter. However, it is not possible to distinguish between cause and effect here, and the possibility remains that females are more likely to conceive when they receive more mate guarding. Male ability to distinguish fertile cycles from nonfertile swellings has also been reported for chacma baboons (Bulger 1993; Weingrill et al. 2003), and sooty mangabeys, *Cercocebus torquatus atys*, where males are able to distinguish fertile swellings from postconception swellings, although these are visually the same (Gordon et al. 1991; Gust 1994). However, Bercovitch (1987) found that male olive baboons did not seem to be able to differentiate between conceptive and nonconceptive cycles.

Behaviour and Paternity Outcome

Mate guarding was typically a strategy of prime-aged, top-ranking males, as in other primate species (e.g. Small 1990; Huffman 1992; Berard et al. 1994). The percentage of mate guarding by a male correlated strongly with the percentage of offspring sired, and an alpha male was more likely to sire when he mate-guarded than when he did not. However, as is generally the case (Hughes 1998), the relation between behaviour and paternity outcome was not perfect: males that were too young to mate-guard still sired, not all sires mate-guarded, and even if the alpha male mate-guarded a female during her entire periovulatory period, he did not necessarily sire the resulting offspring. These discrepancies confirm that females may mate with multiple males per receptive period, indicate the success of sneaky, opportunistic mating tactics by nonalpha males, and mean that mate guarding consistently overestimated the reproductive output of alpha males.

The Priority-of-Access Model

A specific goal of this study was to examine the predictions of the priority-of-access model for mate guarding and paternity outcome. The fit of the observed data was generally good for both mate guarding and for paternity. However, in both cases, the alpha male was more successful than predicted, second- and third-ranking males were less so, and males that were not predicted to mate-guard or sire, because they ranked too low, did both. Alpha males mate-guarded increasingly more than expected as the number of females increased (deviation from the priority-of-access model increased). Paternity deviation from the priority-of-access model was not similarly influenced by the number of females, nor indeed by any of the variables tested. Although paternity patterns will not necessarily be influenced by the same variables as mate guarding, the lack of any explanatory variables is likely also to relate to the inaccuracy of generating paternity predictions for the small numbers of offspring born in any one year based on the degree to which 6-day periovulatory periods overlap.

Alpha male mandrills were more able to monopolize access to receptive females than alpha male yellow baboons are. This difference is unlikely to be caused by differences in group size: the group sizes in the study of yellow baboons (2–14 adult males, 8–24 females) are comparable to those for the mandrills studied here. Although our study groups included fewer adult males (maximum eight), older adolescent male mandrills can outrank older adult males (Setchell 2003), the criterion used for adulthood in baboons, increasing the maximum number of rival male mandrills to 11. Instead, the major difference between these two species appears to be the absence of male–male coalitions in mandrills (Setchell & Wickings 2005), as in chacma baboons (Bulger 1993). According to a model developed recently by Pandit & van Schaik (2003), coalitions are feasible only where competition among males is not too strong, and where costs of coalition formation are moderate. It appears that male competition is simply too strong in mandrills for coalitions to be profitable, and they thus do not occur. Furthermore, in a dense habitat sneaky mating is likely to represent a better strategy than the formation of noisy and conspicuous coalitions against mate-guarding males, because the latter could attract further males that may profit from the situation.

Mate-guarding patterns in mandrills were also more similar to those reported for chacma baboons than for yellow baboons. Although conditions in the colony precluded detailed observation of mate guarding, mate-guarding pairs never changed from the morning to the afternoon observation period, implying that turnover was rare. Where mate-guarding males changed overnight this appeared to be caused by a lack of interest by the alpha male, rather than by challenge by a nonalpha male. Turnover of mate-guarding males is similarly rare in chacma baboons (Bulger 1993), but common in yellow baboons (Noë & Sluijter 1990). Correspondingly, the length of continuous mate guarding (mean 5 days) in mandrills was more similar to the length of consortships in chacmas

(Bulger 1993; Weingrill et al. 2000) than in yellow baboons (Noë & Sluijter 1990). Finally, the majority of female receptive cycles were mate-guarded by only one male in mandrills, as in chacmas (68% of all cycles, 76% of conceptive cycles, Bulger 1993), whereas in yellow baboons many males mate-guard for short periods (Hausfater 1975).

Factors Influencing Alpha Males Monopoly

Our sample includes relatively few group-years, meaning that we were able only to identify major influences on the ability of alpha males to monopolize females. However, in addition to confirming dominance-based priority-of-access to receptive females, we found that reproductive monopoly by the alpha male was negatively related to the number of males present (adult males for mate-guarding monopoly, and all reproductive males for paternity). This reflects a common primate pattern: decreased monopoly as the number of competing males increases has been shown both among and within populations, although it is difficult to disentangle the relative influence of increased numbers of males and females, which are highly correlated (van Noordwijk & van Schaik 2004). Rival males may be resident in a group or a combination of resident and extragroup males. For example, the chance of an individual extragroup male Japanese macaque mating increases when there are many such males, and when a large number of simultaneously receptive females is available relative to the number of resident males (Takahashi 2001). Similarly, multimale influxes in blue monkeys, where multiple extragroup males invade a unimale, multifemale group during the mating season, are rare where population densities, and thus numbers of extragroup males, are low (Cords 2000), and multimale mating in patas monkeys, *Erythrocebus patas*, is related to the availability of extragroup males (Carlson & Isbell 2001). This may be relevant to mandrills, as adult males of this species vary greatly in group association in semicaptivity (Wickings & Dixson 1992; Setchell & Dixson 2001a), and both group-associated and solitary males occur in the wild (Rogers et al. 1996).

Although the number of males influenced alpha male monopolization of receptive females, it was not a significant influence on deviation from the predictions of the priority-of-access model. This implies that an alpha male is able to cope with increasing numbers of rivals, as long as female periovulatory periods do not overlap. However, as group size increases, both the number of simultaneously periovulatory females and the number of males increase. Similarly, in a study of chacma baboons Bulger (1993) found no difference between small (3–5 males) and large (7–11 males) male cohorts either in alpha male consortship success or when the presence of simultaneously receptive females was taken into account. Weingrill et al. (2003) also found that numbers of males and females in chacma baboon groups were poorly related to the consortship success of alpha males. In this study of a population where female interbirth intervals are particularly long, Weingrill et al. suggested that consortship success of alpha males is primarily determined by the number of receptive days a male encountered.

In our provisioned situation, alpha males mate-guarded more than expected as the number of females increased, the opposite of the pattern expected if males experienced mate-guarding fatigue (e.g. Weingrill et al. 2003). This may be partly caused by males being less constrained by food availability than they would be in the wild, and thus able to mate-guard for long periods. However, mate-guarding males clearly adapt their activities to their female partners, their feeding is often interrupted (personal observations), and there is some evidence that alpha males do become less fat across the mating season (Setchell & Dixson 2001b), as reported for rhesus macaques (Bercovitch & Nürnberg 1996; Bercovitch 1997). Competition costs of mate guarding also appear to be high, as mate-guarding males appear highly stressed by the near constant close presence of subordinate rival males, frequently chase and wrestle with rivals, and may receive serious wounds (personal observations).

We found no influence of the duration of alpha male tenure on mate guarding or paternity by alpha males. Studies of other species have shown that newly dominant males may initially have poor mating success (Hausfater 1975; Smuts 1985; Noë & Sluijter 1990). This finding has been related to the need to establish both social relationships with females (Strum 1982; Smuts 1985) and rank relationships with other males (Alberts et al. 2003). Such males also tend to be (but are not always) newly immigrant males, and a partial explanation for the lack of such an effect in these mandrills may therefore be that all animals were familiar with one another in this closed colony. Conversely, male mating success and paternity decrease as male tenure increases in some species, a finding that has been explained by female choice against mating with males that were dominant when the female was immature, and are thus potentially the female's own father (see references in Berard 1999). Again, this was not observed in the mandrill colony, although females did not have the possibility of mating with novel (immigrant) males.

Wild Mandrills

Although several features of the semifree-ranging colony may limit extrapolation of our results to wild mandrills (provisioning, a lack of transfer opportunities for males into and out of groups), we can make some predictions about patterns of male reproductive skew in wild mandrills. Wild groups of mandrills range in size from 15 to hundreds of individuals (Hoshino et al. 1984; Rogers et al. 1996; Abernethy et al. 2002), and even small groups may contain more than one adult male (Hoshino et al. 1984). In smaller groups a single dominant male may be able to mate-guard periovulatory females, and sire the majority of offspring, as in smaller group sizes during this study. However, the largest reported wild groups (mean group size 620) contain a mean of 182 adult females, with 1–17 adult males (mean 7) and 56 males estimated as older than 5 years (Abernethy et al. 2002). Even if each individual female reproduces on average only once every 2 years in the wild, approximately 90 females may be expected to cycle during the same mating season. Female periovulatory cycles are therefore likely to overlap extensively, and dominant males will be unable to control access to all periovulatory females. Furthermore, the dense forest habitat has many visual obstructions, facilitating sneak copulations with nonmate-guarding males, while the costs associated with mate guarding will be far higher in the wild than in our provisioned colony, decreasing both the potential for monopolization, and probably the tenure of dominant males, because of loss of condition. Large group sizes also mean that male dominance ranks are likely to be unstable. Indeed, it seems possible that at least some males may move into and out of the same or different social groups, depending on the presence of receptive females and other males, and their own condition and nutritional requirements (cf. African buffalo, *Syncerus caffer*: Prins 1996), as numbers of males appear to fluctuate over time (Abernethy et al. 2002). Together, these factors are likely to decrease the monopolization of receptive females by individual males in the wild by comparison with this captive situation. Tests of these predictions will require studies of wild populations at levels that are currently not possible.

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