MATE CHOICE IN MALE MANDRILLS (*MANDRILLUS SPHINX*)

Authors: Joanna M Setchell [1,2] and E Jean Wickings [2]

Institutions: [1] Department of Biological Anthropology, University of Cambridge, Downing Street, Cambridge CB2 3DZ, UK

[2] Centre International de Recherches Médicales, BP 769, Franceville, GABON

Running title: Setchell & Wickings: Male mate choice in mandrills

Correspondence to:

Dr Joanna M Setchell
Department of Biological Anthropology
University of Cambridge
Downing Street, Cambridge CB2 3DZ, UK
Tel: +44 (0)1223 335454, Fax: +44 (0)1223 335460
Email: mandrills@yahoo.co.uk

ABSTRACT

Male primates that attempt to monopolise access to receptive females by mate-guarding expend time and energy and risk injury, making reproduction costly. Males should therefore show mate choice, and preferentially allocate mating effort to females that are likely to be fertile and those that will produce high quality offspring. Specifically, males should preferentially mate-guard high-ranking females rather than low-ranking females, as they are more likely to be fertile and are able to invest more in offspring. Males should also prefer parous females to primipares, for similar reasons. Finally, males should avoid mating with close relatives, to avoid the deleterious effects of inbreeding. We investigated 13 group-years of mate-guarding observations for two semi-free-ranging groups of mandrills to examine the influence of these factors on male investment in mate-guarding. We found that males mate-guarded higher-ranking females more than lower-ranking females, and parous females more than nullipares. Female age, true relatedness and maternal kinship did not influence male mate-guarding. Our results suggest that male mandrills do exercise mate choice for higher-quality females, in the form of higher-ranking and parous females. As alpha males are responsible for the great majority of mate-guarding, this can lead to assortative mating, where high-ranking males reproduce with high-ranking females, and has important implications for social relationships and kin selection.

KEYWORDS: mate choice, parity, mate-guarding, mating effort, non-human primates

INTRODUCTION

Sexual selection theory has traditionally concentrated on male-male competition and female mate choice (Bradbury & Davies 1987). However, where the general rule of high female investment is reversed and males provide the majority of parental care, sex-role reversal can occur, and females may compete for males (review in Andersson 1994; Petrie 1983). Evidence is also increasing for the occurrence of mate choice by males and female-female competition for mates in species without sex-role reversal (Engqvist & Sauer 2001; Gowaty 2003; Koeninger & Altmann 2001). In many species, then, both males and females may be expected to engage in competition for mates and to show mate choice (Cunningham & Birkhead 1998; Johnstone et al. 1996; Kraak & Bakker 1998).

Although female primates invest substantially more in reproduction than males do, reproduction can also be costly for males. Males that attempt to monopolise access to receptive females risk injury in contest competition (Drews 1996), and face constraints on foraging activity which are likely to result in decreased energy intake (e.g. Alberts et al. 1996; Bercovitch 1983). Moreover, sperm production is costly and sperm delivery and ejaculate quality are compromised by successive ejaculations (Dewsbury 1982; Marson et al. 1989; Preston et al. 2001; Wedell et al. 2002). To maximise their reproductive success, therefore, males should show mate choice, apportioning costly mating effort in relation to the quality of an individual female and cycle, and preferentially competing for the most fertile, and those that will produce the highest quality offspring. Specifically, males are expected to mate-guard females when they are most likely to be fertile, and to mate-guard conceptive cycles in preference to non-conceptive cycles, if they are able to distinguish between the two (e.g. Bulger 1993; Weingrill et al. 2003). Males should also preferentially mate-guard high-ranking females vs. low-ranking females (Berenstain & Wade 1983), because such females are likely to be more fertile and more able to invest more in resulting offspring. Males should prefer parous females to nullipares for similar reasons (Anderson 1986; Smuts 1987). Finally, males may be expected to avoid mating with close kin, due to the deleterious effects of inbreeding on offspring (Alberts & Altmann 1995; Constable et al. 2001; Takahata et al. 1999).

Mandrills are one of the most sexually dimorphic primate species, suggesting that male-male competition for access to peri-ovulatory 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. The extent of development of male secondary sexual characters varies extensively between adult males (Wickings & Dixson 1992) and is related to dominance rank, with the alpha male possessing the most developed secondary sexual characters (Setchell & Dixson 2001a). 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 (Abernethy et al. 2002; Harrison 1988). Most of our knowledge of reproduction in this species therefore comes from a semi-free-ranging colony of animals at the Centre International de Recherches Médicales, Franceville (CIRMF), Gabon, which provides a unique opportunity to study this little-known species under naturalistic conditions. Studies of this colony show that multiple males associate with the social group of females and their young (Setchell & Dixson 2001a; Wickings et al. 1993), and observations from the wild confirm this multi-male, multi-female social system (Abernethy et al. 2002).

The dominant male in a mandrill group has the highest levels of circulating testosterone, and exhibits the brightest and most extensive red coloration, while other males show lower testosterone levels, and less brightly coloured skin (Setchell & Dixson 2001a)*.* Only males aged 8+ yr mate-guard, with *a*lpha males accounting for 77-100% of peri-ovulatory mate-guarding activity, and 33-100 % of paternity in a mating season (Setchell et al. 2005a). Mate-guarding appears to be costly: alpha males lose “fattedness” across the mating season (Setchell & Dixson 2001b), appear highly stressed by the near constant close presence of subordinate males, frequently chase and wrestle with rivals, and may receive serious wounds (unpublished observations).

We have recently used 13 group-years of behavioural observations to show that male mandrills preferentially mate-guard on days when females are most likely to be fertile, and mate-guard conceptive cycles in preference to non-conceptive cycles (Setchell et al. 2005a). Here we investigate the same data set in more detail to examine further factors that may influence male investment in mate-guarding, specifically female rank, parity and age, and relatedness between the female and the mate-guarding male.

METHODS

Study Animals

The CIRMF mandrill colony was established in 1983/4, when 15 animals (7 males, 8 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 semi-free-ranging group was established in a smaller enclosure (E2, 3.5 ha) by transferring 17 mandrills (including 6 adult females and 4 adult males) from the first enclosure. The animals forage freely and receive daily supplements of monkey chow, fruit and vegetables, designed to provide 100% of their nutritional requirements (calculated according to the mass and the age-structure of the group). Water is always available from a stream, which runs through both enclosures. Behavioural observations are made twice daily (approx. 10h00-11h30 and 15h30-17h30) 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 eight year period 1996-2003. The size and age-sex composition of the study groups during this period is shown in Table 1 and corresponds to the smaller end of group sizes observed in the wild (Rogers et al. 1996). 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 available for mandrills, but studies of baboons have shown that increase in sexual swelling size co-occurs with increased estrogen levels during the follicular phase of the menstrual cycle (Shaikh et al. 1982; Wildt et al. 1977). A rapid decrease in sexual swelling size (break-down) coincides with a post-ovulatory rise in progesterone, and the swelling detumesces during the luteal phase until it is flat. Cycle days were numbered according to proximity 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 mate-guarding to the six days before swelling break-down, termed the “peri-ovulatory period”, which encompasses the period during which ovulation and conception are most likely to occur (Hendrickx & Kraemer 1969; Shaikh et al. 1982; Wildt et al. 1977). 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

Opportunities for behavioural data collection are limited due to the dense nature of the forested enclosures, and systematic, focal observations of individual animals are not possible, precluding detailed examination of male-female interactions during the peri-ovulatory period. We therefore used the occurrence of mate-guarding as an estimate of male attempts to secure unique access to a receptive female. Mate-guarding is a readily observed, unambiguous behaviour in mandrills, where a male follows a female closely and persistently, interacts with her sexually, and attempts to prevent other males from doing so. The dominant male in a group is responsible for the great majority of mate-guarding behaviour, but other males may also mate-guard (Setchell et al. 2005a). As there are more sexually active males than there are females cycling on any one day (Setchell et al. 2005a), the occurrence of mate-guarding can be regarded as a useful measure of male sexual interest (Setchell & Wickings 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 never observed to change during an observation session, or 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 in close proximity to the females at night. We therefore assumed that mate-guarding continued outside observation periods.

Cycles for which observations were available for fewer than four of the six peri-ovulatory days were discarded from analyses. Observations were available for four or more peri-ovulatory days for 171 female cycles, from 44 females, over 13 group-years (mean±sem 3.9±0.5 cycles per female, range 1-16, distribution across the years of the study is shown in Table 1).

Dominance Hierarchies

Rank relations between males and between females were determined using *ad libitum* records of avoidance behaviour during daily observation periods, resulting in the construction of a square interaction matrix in which entries below the diagonal (representing a dominant animal that avoided a subordinate) were few or zero. Female dominance ranks determined in this manner are stable and matrilineal in mandrills (Setchell 1999), and were expressed as the percentage of females over three years of age dominated to account for demographic changes over time (Cheney et al. 1988). The identity of the alpha male was always clear: all other males avoided this individual, who never avoided other males.

Relatedness Coefficients

The founder individuals of the CIRMF colony were all unrelated (Wickings 1995). Coefficients of relatedness were therefore directly calculated for pairs of animals using the known pedigree for the colony (based on microsatellite paternity analysis, see Charpentier et al. 2005). The relatedness coefficient between mother-son and father-daughter pairs is 0.5, full-siblings are 0.5, half-siblings are 0.25 etc.

As there has been no subsequent addition of new animals to the CIRMF colony since its foundation, the animals may be more closely related to one another than in groups in the wild. The most inbred infants in the CIRMF colony are currently the offspring of half-siblings (inbreeding coefficient IC=0.25, Charpentier et al. unpublished data). Individual males and females contributing to this study were related at a maximum of 0.50 (full siblings). Mean relatedness between females and dominant males, who are responsible for the great majority of mate-guarding, was 0.12±0.01 (n=163 female cycles). How this reflects the situation in the wild is unknown, as relatedness within groups in the wild is completely unknown.

Data Analysis

The occurrence of mate-guarding during a peri-ovulatory period was measured as the % of days that a female was observed that she was mate-guarded. We examined the effects of female rank, age and parity (nulliparous vs. parous) on the occurrence of mate-guarding during an individual cycle using weighted least squares regression analysis (GLM Univariate procedure in SPSS 11.0), first verifying that the data were normally distributed (skew / standard error of skew <3, Zar 1996). We also included whether a cycle overlapped with peri-ovulatory periods in other females ("overlap" = presence vs. absence of simultaneously peri-ovulatory females), and whether or not a cycle was conceptive in the model, as we have previously shown that these variables significantly influence the occurrence of mate-guarding (Setchell et al. 2005a). Some females contributed multiple cycles, leading to pseudo-replication and an artificially inflated sample size. We therefore weighted each cycle's contribution to the estimate of linear regression equations as an inverse function of the number of cycles that the individual female contributed to the data set (i.e. weights were calculated as equal to 1/n where n is the number of cycles for the female concerned). The degrees of freedom reflect the number of independent females contributing (n=44), rather than the total number of cycles used in the analysis. This enabled us to calculate a regression equation that considered all data, but ensured that each female contributed equally to its estimation, regardless of the number of cycles she contributed. An analogous solution to a similar problem can be found in Manson et al (2004).

A similar analysis was performed for the % of days that a female was observed that she was mate-guarded by the alpha male, including relatedness to the female as an additional covariate. Relatedness was measured as both the relatedness coefficient between the alpha male and each mate-guarded female, and also as the maternal relationship between the two (mother-son and maternal sibling dyads: 1, other dyads: 0). Kinship was analyzed only for alpha male mate guarding because alpha males were responsible for the great majority of mate-guarding (see results), and too few data were therefore available for analysis of relatedness between non-alpha males and the females that they mate-guarded.

RESULTS

The presence of simultaneously peri-ovulatory females, female rank and female parity all influenced how much a female was mate-guarded (Table 2). Females were more likely to be mate-guarded if no other females were simultaneously peri-ovulatory, high-ranking females received more mate-guarding than low-ranking females (illustrated in Fig. 1), and parous females received significantly more mate-guarding than nullipares (illustrated in Fig. 2). There was a trend towards conceptive cycles receiving more mate-guarding than non-conceptive cycles, but this was non-significant. Female age did not significantly influence mate-guarding (Table 2).

Alpha males contributed overwhelmingly to peri-ovulatory mate-guarding (258 of 275 days observed, 94 %). Repeating the above analysis using only mate-guarding by alpha males thus produced very similar results to the analysis for all males (Table 2). The degree of relatedness between the alpha male and the female varied from 0 (n=111 peri-ovulatory periods) to 0.5 (full-siblings, mother-son or father-daughter pairs, n=22 peri-ovulatory periods), but did not significantly influence whether the alpha male mate-guarded a female (Table 2). Replacing the relatedness variable with one that described only maternal relatedness (mother-son and maternal sibling dyads: 1, other dyads: 0) did not alter the significance of these results (Table 2).

DISCUSSION

Our results suggest that male mandrills do exercise mate choice for high quality females. Males were more likely to mate-guard higher-ranking females than they were lower-ranking females. Preference for high-ranking females increases a male’s reproductive success, as offspring of higher-ranking females will be of higher quality. Higher-ranking females are able to invest more in offspring, raising infants that are heavier for their age than those of lower-ranking females (Setchell et al. 2001). Moreover, daughters of high-ranking mothers inherit their high-rank, leading to advantages in resource acquisition, and increased fecundity when compared with lower-ranking females (Setchell et al. 2005b; Setchell et al. 2002). Finally, although infant survival is high for all ranks in this semi-free-ranging colony (Setchell et al. 2002), under wild conditions offspring survival may also vary with social rank. For example, infants of higher-ranking female long-tail macaques (*Macaca fascicularis*) are more likely to survive than those of lower-ranking females (van Noordwijk & van Schaik 1999), and low-ranking female primates tend to occupy peripheral positions in the social group, leading to higher predation risk (e.g. Dittus 1977; Ron et al. 1996; van Noordwijk & van Schaik 1987).

Male choice for high-ranking females has been demonstrated for many other primate species (earlier studies are reviewed by Berenstain & Wade 1983; see also de Ruiter et al. 1994; Kuester & Paul 1996). As dominant males are the most able to express mate choice, this can lead to assortative mating, where high-ranking males reproduce with high-ranking females, with important implications for social relationships and kin selection. Social bonds in cercopithecine species have long been known to follow maternal relatedness (e.g. Gouzoules & Gouzoules 1987). However, recent studies have shown that paternal half-sisters in both rhesus macaques (Widdig et al. 2001) and baboons (Smith et al. 2003) are also more affiliative towards each other than they are to unrelated females. Under conditions of assortative mating, members of high-ranking matrilines, which are the most attractive, and therefore reproduce with the alpha male, will be more closely paternally related to one another than those of low-ranking matrilines, where females are less attractive, and more likely to reproduce with other males, but not necessarily with the same male. Members of different high-ranking matrilines will also be more paternally related to one another than they are to members of low-ranking matrilines, or than members of different low-ranking matrilines are to one another. These differences between high- and low-ranking matrilines may have important consequences for the strength of female alliances (Silk & Boyd 1983).

Males also mate-guarded parous females significantly more than nullipares. Again, this may represent male choice for females that will produce higher quality offspring: offspring of primiparous females are lighter for their age than those of parous females (Setchell et al. 2001). Mate-guarding was not influenced by female age, despite the fact that females continue to invest in their own growth for several years after they begin their reproductive careers (Setchell et al. 2001), and that younger females may therefore have fewer resources to invest in their offspring. Finally, we found no influence of close kinship on mate-guarding. Alpha males did not appear to base mate-guarding decisions on either kin recognition (e.g. via phenotype matching, Alberts 1999; Smith et al. 2003; Widdig et al. 2001), or simply on matrilineal membership. This may be because females should avoid inbreeding more actively than males, due to differential investment in offspring (Trivers 1972), and differential opportunity costs of producing an inbred offspring to males and females (Clutton-Brock & Harvey 1976). This prediction is upheld by data reported for other primates, where sexual behaviour between close relatives is almost always initiated by males (Pusey 1990). For example, while paternity analyses have demonstrated inbreeding avoidance in captive macaques (Inoue et al. 1990; Smith 1995), behavioural studies have shown that it is females that are responsible for avoiding mating (Soltis et al. 1999). However, Manson & Perry (1993) found that male rhesus macaques did discriminate between related and unrelated females, courting the latter more intensively, although they were less averse to inbreeding than females were.

A final issue that remains to be resolved in mandrill mate choice is whether “friendships” or special relationships occur between individual males and females, as described for other species of primate living in multi-male, multi-female groups such as baboons (Altmann 1980; Seyfarth 1978; Smuts 1985), rhesus macaques (Chapais 1983) and Japanese macaques (Takahata 1982). We currently lack the detailed behavioural data that would allow us to determine whether long-term relationships between males and females exist, and whether these are reflected in mating preferences. It seems unlikely that this occurs at the level of mate-guarding, as the alpha male is always responsible for the great majority of this behaviour. However, such relationships may influence the occurrence and success of sneaky mating tactics.

ACKNOWLEDGEMENTS

We wish to thank the Centre International de Recherches Médicales and the staff of the Primate Centre for making this study possible. The CIRMF is financed by the Gabonese government, Total Gabon and the Ministère Français des Affaires Etrangères. We are grateful to Marie Charpentier for access to the mandrill pedigree. JMS was supported during parts of the data collection by a research studentship from the Medical Research Council, UK and a CIRMF internship, and during data analysis and writing of the manuscript by a Leverhulme Trust project grant award to Leslie Knapp, Department of Biological Anthropology, University of Cambridge. The manuscript was improved by helpful comments from two reviewers.

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Table 1: Composition of the study groups, with numbers of cycles and conceptions

Year	Adult males [1]	Older adolescent males [2]	Younger adolescent males [3]	Reproductive females [4]	Juveniles and infants	Total group size	Number of cycles
Enclosure 1							
1996	1	4	6	13	12	36	18
1997	3	5	6	13	20	47	15
1998	5	4	8	19	29	65	14
2000	8	1	12	22	24	69	17
2001	6	3	12	27	28	81	18
2002	8	3	14	31	48	104	25
2003	5	2	7	19	36	69	18
Enclosure 2							
1996	5	0	4	6	6	21	9
1997	4	2	2	6	14	28	2
1998	4	2	3	10	11	30	4
2000	4	0	5	13	14	36	8
2001	4	0	6	13	21	44	5
2002	4	2	5	15	26	52	14
2003	3	3	6	16	14	42	4

based on ages at 01 May, the approximate beginning of the mating period

[1] Adult males: males aged >10.0 yr

[2] Older adolescent males: males aged 8.0 to 10.0 yr

[3] Younger adolescent males: males aged 3.8 to 8.0 yr

[4] Reproductive females: females undergoing reproductive cycles

Table 2. Results of weighted least squares regression analysis to test for the influence of simultaneous peri-ovulatory periods, conception, female rank, female parity and relatedness to the alpha male on the percentage of peri-ovulatory days that a female cycle was mate-guarded by all males and by alpha males

Source	**All males**		**Alpha males, using true relatedness**		**Alpha males, using maternal relatedness**	
	$F_{1,39}$	**Significance**	**$F_{1,38}$**	**Significance**	**$F_{1,38}$**	**Significance**
Overlap [1]	12.830	0.001	19.653	<0.001	20.102	<0.001
Conception	3.167	0.083	4.069	0.051	2.699	0.109
Female rank	4.841	0.034	4.078	0.050	4.054	0.051
Female parity [2]	4.059	0.051	6.591	0.014	1.679	0.203
Female age	0.033	0.857	0.134	0.716	0.429	0.517
Relatedness [3]	--	--	2.892	0.097	1.362	0.250

Each cycle's contribution to the analysis was weighted as an inverse function of the number of cycles that the individual female contributed to the data set. df reflect the number of independent females contributing, rather than the total number of cycles analysed.

[1] Overlap: whether other females were simultaneously peri-ovulatory

[2] Female parity as nulliparous vs. parous females

[3] Degree of relatedness between the alpha male and the female was measured as true relatedness, and also as maternal relatedness only (mother-son and maternal sibling dyads: 1, other dyads: 0)

FIGURE LEGENDS

Fig. 1. Mean±SEM % mate-guarding per cycle vs. female rank. “Low” represents the lowest 25%, “mid” the middle 50%, and “high” the top 25% of female ranks. Some females contributed more than one cycle to the data set

Fig. 2. Mean±SEM % mate-guarding per cycle vs. female parity. Some females contributed more than one cycle to the data set

Fig. 1

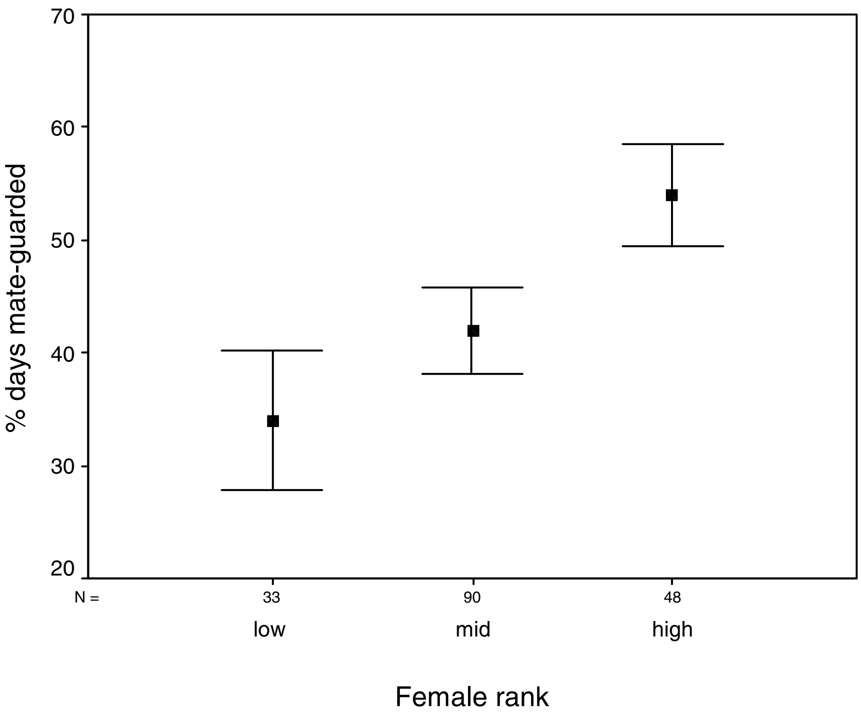
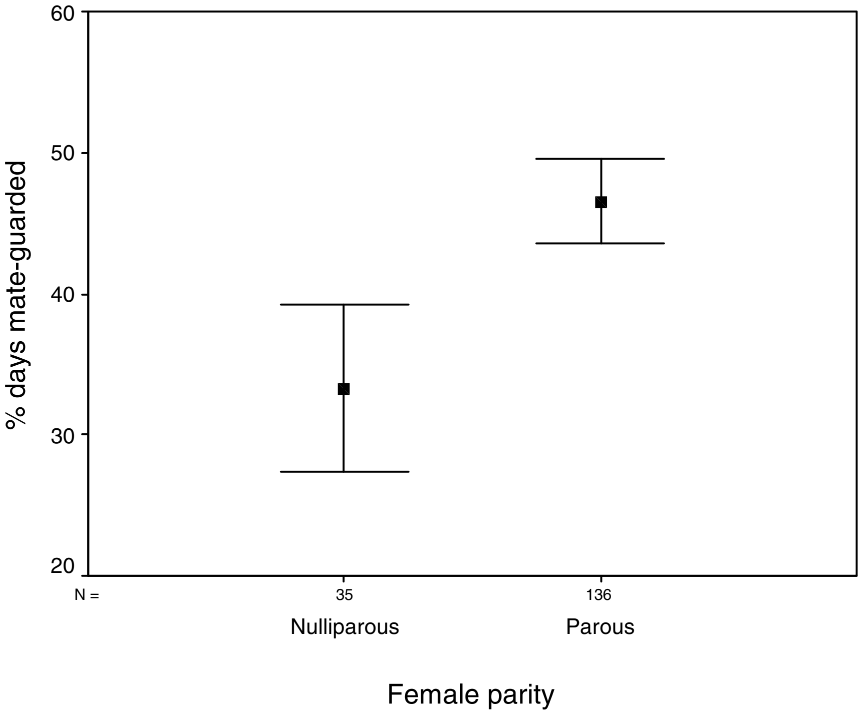

70
60
50
40
30
20
% days mate-guarded
N =
33
90
48
low
mid
high
Female rank

Fig 2.


60
50
40
30
20
% days mate-guarded
N =
35
136
Nulliparous
Parous
Female parity