

Mating System in Mouse Lemurs: Theories and Facts, Using Analysis of Paternity

Marjorie Andrès^a Michel Solignac^b Martine Perret^a

^a UMR 8571, Département d'Ecologie et Gestion de la Biodiversité, CNRS, Brunoy,

^b Laboratoire Populations, Génétique et Evolution, CNRS, Gif-sur-Yvette, France

Key Words

Sociosexual behaviours • Reproductive success • Dominance • Mate choice •
Microsatellites • Mouse lemur • *Microcebus murinus*

Abstract

Among nocturnal Malagasy prosimians, the grey mouse lemur (*Microcebus murinus*) is considered a solitary species which has a promiscuous mating system. Indirect indicators, such as the lack of sexual dimorphism, the overlapping of male and female home ranges with each other, the synchronism of seasonal oestrus and the high relative testes size of males, support the presence of sperm competition. In captivity, an intense sexual precopulatory competition develops among males, leading to the emergence of a dominant male who fathers the majority of the litters. Although multiple mating did occur, the dominant male achieved the majority of the matings on the first day of oestrus. A 'mate-guarding' behaviour, exhibited by the dominant male, was observed in 11 groups out of 15, on only the first day of the vaginal opening and was significantly more often directed towards younger females. Females also played an important role in sexual competition among males, since their presence enhances the aggressive interactions between males. Difference in aggressive behaviours of females, in response to male sexual solicitations, suggests female mate choice. Compared with data from wild animals, it may be hypothesised that alternative mating strategies can be used by male grey mouse lemurs to enhance their reproductive success, depending on the availability and distribution of receptive females.

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Fax +41 61 306 12 34
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Martine Perret, CNRS UMR 8571
Département d'Ecologie et Gestion de la Biodiversité
4, avenue du petit château, FR-91800 Brunoy (France)
Tel. +33 1 60 47 92 00, Fax +33 1 60 46 81 18
E-Mail martine.perret@wanadoo.fr

Introduction

The theory of sexual selection was defined first by Darwin [1871] and implies two different mechanisms: intrasexual competition, in which individuals of the same sex compete for access to the other sex, and mate choice. While the first mechanism generally concerns males, mate choice generally concerns females, according to the differential reproductive investment by the males versus females [Trivers, 1972]. Because males make a smaller parental investment than females, their reproductive success is limited by the number of females they can inseminate, implying that they compete for priority of access to reproduction [Darwin, 1871; Trivers, 1972].

Intrasexual competition among males may occur both by precopulatory competition, involving contest competition, and postcopulatory competition, primarily sperm competition [Kappeler, 1997a, b]. Differences in the relative intensity of pre- and postcopulatory competition depend on the ability of males to monopolise access to receptive females, which in turn depends on both the number and the spatial distribution of females and the degree of oestrus synchrony [Altmann, 1962; Ridley, 1986; Dunbar, 1988; Altmann, 1990; Mitani et al., 1996a; Kappeler, 1997b; Radespiel et al., 2001; Eberle and Kappeler, 2002].

Precopulatory competition involves contest competition by physical combats and scramble competition by competitive mate searching [Clutton-Brock, 1989; van Hooff and van Schaik, 1992; Radespiel et al., 2001, 2002; Eberle and Kappeler, 2002]. When males directly compete, social dominance has been predicted to play an important role in regulating access to fertile females because high-ranking males will be able to monopolise oestrous females more effectively than lower-ranking competitors ('priority-of-access' model [Cowlshaw and Dunbar, 1991; de Ruiter and van Hooff, 1993; Dixson, 1998]). However, female mate choice, which may be an important factor regulating the sexual competition among males, and the alternative mating strategies of subordinate males may dilute the effects of dominance and contribute to the equivocal relationship between male dominance rank and reproductive success [Smuts, 1987; Small, 1993; Harcourt, 1996; Soltis et al., 1997].

Within gregarious Malagasy prosimians, multiple mating strategies have been observed, but field observations on sexual encounters during the breeding season have indicated the importance of female choice in the reproductive success of males, regardless of the mating strategy [Pereira and Weiss, 1991; Richard, 1992; Pereira and McGlynn, 1997]. Within nocturnal Malagasy species, it is more difficult to obtain direct observations on sexual interactions. The grey mouse lemur (*Microcebus murinus*), a small (60–80 g), arboreal primate, usually considered a solitary species, is one of the best-studied nocturnal species in both field and captive conditions. It exhibits behavioural and physiological seasonal rhythms to cope with seasonal changes both of climatic conditions and resources on which it feeds. During the cold and dry winter, both sexes are sexually quiescent and become less active. The short breeding season is restricted to the hot and rainy summer months, and is associated with sustained behavioural and physiological activities. This seasonal breeding pattern is triggered by variations in the photoperiod [Perret, 1992; Perret and Aujard, 2001]. Mouse lemurs are typically long-day breeders: in males, plasma testosterone levels increase from 5 to 60 ng/ml about 2–3 weeks following photoperiod activation, and females enter oestrus almost synchronously within 4–5

weeks following the onset of long day length [Perret and Aujard, 2001]. In females, the vulva remains closed except during the oestrous period of 3–5 days. During the short pro-oestrous period, a prominent vaginal swelling develops and females are highly attractive to males.

Indirect evidence from trapping data and observations on the operational sex ratio in wild populations suggests ‘scramble competition polygyny’ [Kappeler, 1997a; Fietz, 1999; Radespiel et al., 2001; Eberle and Kappeler, 2002]. Because male and female home ranges exhibit a substantial overlap, it is believed that both sexes encounter multiple partners. Moreover, the absence of sexual dimorphism and the short breeding season with oestrus synchrony are strong indicators of weak precopulatory sexual competition among males who cannot monopolise access to oestrous females. Lastly, the relatively large size of the testes seen in most nocturnal Malagasy primates suggests the presence of sperm-based scramble competition [Harcourt, 1996; Dixson, 1998]. However, it has been suggested that social dominance may regulate reproductive decisions. Martin [1972] hypothesised that dominant males might exclude subordinate males from the centre of population nuclei containing the reproductive females. In captivity, when grey mouse lemurs are grouped heterosexually, oestrus synchrony and the short period of female receptivity lead to an intense competition between males for priority of access to fertile females [Andrès et al., 2001]. By combining both behavioural and genetic paternity data, this paper aims to further clarify the mating system of the grey mouse lemur.

Material and Methods

Study Animals

All mouse lemurs used in this study (45 males and 30 females) were born in the breeding colony established at Brunoy (MNHN, France, European Institutions Agreement No. 962773) from a stock originally caught near the southern coast of Madagascar, 30 years ago. Captive animals were kept in controlled conditions with constant ambient temperature (24–26°C), constant relative humidity (55–60%) and food available ad libitum (standardised diet including fresh fruit, a home-made milky mixture and meal worms). All experiments were carried out in accordance with the European Communities Council Directive 86/609/EEC.

Biological rhythms of mouse lemurs are photoperiod dependent [Perret et al., 1998; Perret and Aujard, 2001]. To ensure highly synchronised changes in biological rhythms among individuals, captive animals were routinely exposed to an artificial photoperiodic regimen consisting of a 5-month period of Malagasy summer-like day length (14 h light/day) followed by a 3-month period of Malagasy winter-like day length (10 h light/day). In such conditions, breeding state is acquired within 4 weeks following the exposure to long day length.

Behavioural Measurements

Two weeks after the beginning of the breeding season, induced by exposure to long days, 15 groups of 3 males were constituted and kept in cages (150 × 120 × 70 cm) with many wooden supports and several nests. Males were 2–4 years old (mean = 2.4 ± 0.3 years, n = 18) and weighed on average 82 ± 2 g. Two females were introduced one by one into each group when they entered advanced pro-oestrus (4–5 days before the vaginal opening).

One week after the formation of the group, daily observation sessions began until both females finished their oestrus. Owing to the oestrus synchrony, observation sessions usually covered a 10- to 12-day period. In each group, behavioural activities were recorded by videotaping using an infrared camera during the first 60 min of nocturnal activity. Video-

tapes were viewed and behavioural items were scored for each individual. Recorded behaviours included:

- agonistic activities: chasing (one animal forces another to flee to the ground or to enter a nest), fighting (one animal struggles with another; fights may be associated with bites, but in our study no instance of physical injury occurred); in fact, a chase or a fight immediately stopped when the chased animal, considered the ‘loser’, entered a nest;
- marking behaviours: urine washing, anogenital rubbing and muzzle wiping;
- sexual behaviours: sniffing or licking female genitalia, sexual pursuit, mount with or without copulation, ‘mate-guarding’ behaviour (one male remained close to the female and chased all the males that attempted to approach her); effective copulation was confirmed by the presence of spermatozoa in vaginal smears.

To assess the rank for each male of each group, a dominance index was calculated based on the outcomes of fights won (W) or lost (L) during the total observation period using the formula: $(W - L)/(W + L)$. This index varies from +1 for a male that is never attacked and whose aggressive interactions are always successful, to -1 for a male that never initiates fights and is always chased by other males. This dominance index permits the comparison of individuals living in different social groups. The details of the sociosexual behaviours were recorded in only 6 groups of 3 males, but the precise number of mounts and observation of the mate-guarding behaviour were recorded in 15 groups of 3 males.

Lastly, both males and females were weighed twice during the observation period, and the mean body mass was used for statistical analysis.

Genetic Determination of Paternity

The thirty study females had 27 litters, yielding 55 infants. DNA was extracted from individuals by taking ear punches, using the QIAamp DNA Mini Kit (Qiagen). The random amplified polymorphic DNA method was used for genetic determination of paternity in 17 litters, as described in Andrès et al. [2001]. For the 10 remaining litters, microsatellites were used to determine paternity. We amplified the DNA of each individual for 12 nuclear microsatellite loci: 7 from Radespiel et al. [2002] and 5 from Manfred Eberle [pers. commun.]. We assessed PCR reactions in 10 μ l of reaction medium containing 5–10 ng DNA template, 400 nM of each primer, 75 μ M each of dGTP, dCTP and dTTP, 6 μ M dATP and 0.1 μ Ci (= 3.7×10^3 Bq) [α^{33} P]dATP, 1.5 mM MgCl₂, 2 μ g bovine serum albumin, 1 \times reaction buffer and 0.4 units of Promega *Taq* polymerase. After a denaturing step of 3 min at 94°C, samples were processed through 35 cycles consisting of 30 s at 94°C, 30 s at 55°C and 30 s at 72°C. The last elongation step was lengthened to 10 min. Amplified DNA was denatured for 5 min at 95°C with 5 μ l of denaturing blue and electrophoresed on 6% denaturing polyacrylamide sequencing gels. Gels were dried and exposed to X-ray films for 24–48 h.

Statistical Analysis

Behavioural items were presented as means per 60 min \pm SEM. Data were tested for normality (skewness and kurtosis tests, Systat) or transformed for normality if required. Statistical differences between parameters were tested using multiway analysis of variance followed by a Tukey post hoc test on least square adjusted means. Possible relationships between behavioural parameters were assessed using the Spearman rank correlation.

Results

Dominance and Sociosexual Behaviours

Agonistic Activities. Social relationships between males within a group were based on agonistic behaviours. According to the decreasing value of the dominance index in each group, males were ranked as α male (mean index: 0.806 ± 0.1), β male (mean index: -0.290 ± 0.2) and γ male (mean index: -0.870 ± 0.05). The number of aggressive outcomes performed by α males was significantly higher than

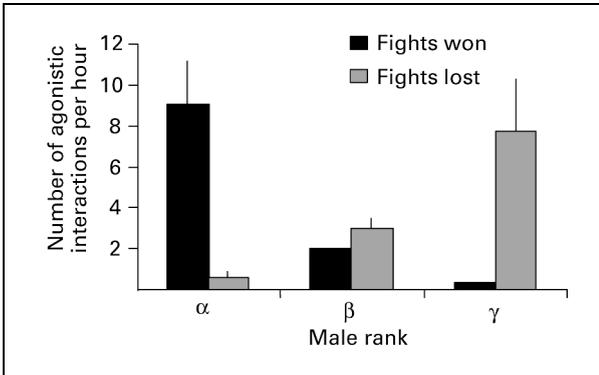


Fig. 1. Frequency (mean per hour \pm SEM, $n = 6$) of agonistic interactions between grouped males according to their rank: α , β and γ from the highest to the lowest rank.

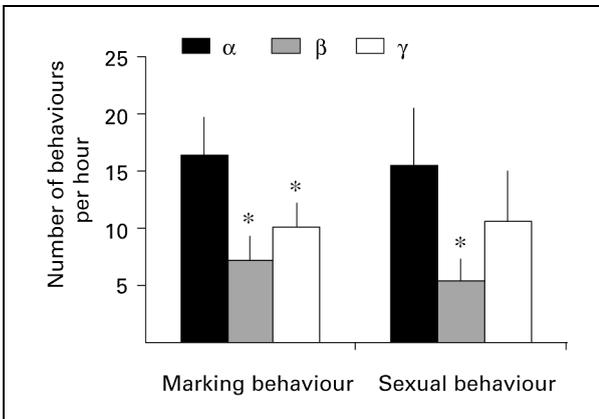


Fig. 2. Frequency (mean per hour \pm SEM, $n = 6$) of marking and sexual behaviours according to male rank. * $p < 0.05$, compared to values of dominant males.

those recorded in β and γ males ($F_{2, 15} = 19.2$, $p < 0.001$; fig. 1). No significant correlation was found between rank and body mass ($r = 0.176$, $n = 18$, $p > 0.1$) or rank and age ($r = -0.072$, $n = 18$, $p > 0.1$). Agonistic relationships between males were similar in all groups. The α male directed more than twice the number of agonistics acts towards the β male as vice versa (66 vs. 24%). Behavioural reversals between the α and γ male and the β and γ male were extremely rare (1 and 10%, respectively). Thus, relationships can be described as despotic dominance expressed by the α male.

Marking Behaviours. The marking behaviour engaged in most frequently by male mouse lemurs was urine washing. This represented more than 80% of the total number of observed marking behaviours. All marking behaviours were thus in-

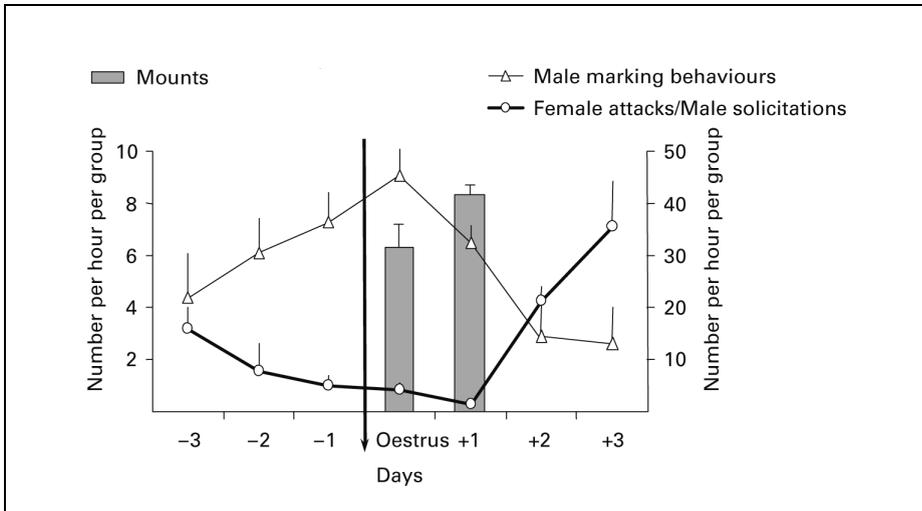


Fig. 3. Temporal distribution during the peri-oestrous period of male behaviours (mounts and marking behaviours, frequency per hour and per group \pm SEM, $n = 15$). Females' agonistic behaviours are indicated by the ratio of female attacks in response to male solicitations. Days are dated from the vaginal opening underlined by an arrow.

cluded in the same behavioural category. Marking frequency differed according to male rank ($F_{2, 15} = 3.77$, $p < 0.05$; fig. 2) and was significantly higher in α males than in β and γ ones who exhibited a similar lower frequency ($p < 0.05$). Within a group, α males performed on average $54.1 \pm 8\%$ of all marking behaviours recorded in each group. Significant positive correlations were found between dominance index and the number of marking behaviours ($r = 0.581$, $n = 18$, $p < 0.01$) and between marking and aggressive behaviours ($r = 0.626$, $n = 18$, $p < 0.05$).

Sexual Behaviours

Four behaviours were considered as 'sexual' interactions: sniffing or licking genitalia of females, sexual pursuits, mounts with or without copulation and mate-guarding behaviour. The temporal distribution of sexual behaviour was examined in relation to females' behaviours and oestrus time (fig. 3). All the mounts occurred on the first and the second day of vaginal opening ($D_7 = 0.714$, $p < 0.001$). By contrast sexual pursuits began earlier and stopped 2 days after the vaginal opening. Marking and sniffing behaviours seemed to follow the same pattern since these behaviours reached their minimum 2 days after oestrus ($KS_7 = 1.0$, $p < 0.001$). In response to male sexual solicitations, females attacked males vigorously. Females demonstrated a significantly higher body mass than males did (average: 91 ± 3 g, $n = 12$, $F_{1, 28} = 4.8$, $p < 0.03$), and they consistently won agonistic encounters with males. Female agonistic behaviours were highly correlated with sexual solicitations ($r = 0.645$, $n = 18$, $p < 0.01$), but no correlation was found with dominance index ($r = 0.190$, $n = 18$, $p < 0.1$). Lastly, the ratio of female attacks following male sex-

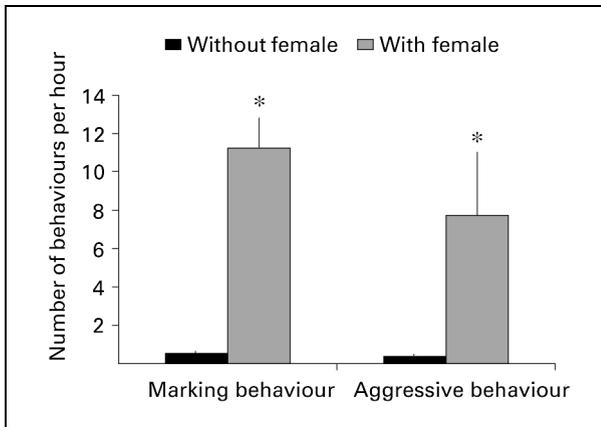


Fig. 4. Frequency (mean per hour \pm SEM, $n = 6$) of marking and agonistic behaviours of grouped males before and after the introduction of an oestrous female. * $p < 0.001$, compared to values of males grouped without females.

ual solicitations strongly increased after the second day of vaginal opening when females refused all sexual interactions with males (fig. 3).

The frequency of sexual behaviours was significantly higher in α males than in β and γ males ($KW = 5.9$, $p < 0.05$; fig. 2). Within a group, α males performed $66.5 \pm 5\%$ of all sexual behaviours recorded in a group. The number of male sexual solicitations towards females was strongly correlated with dominance index ($r = 0.647$, $n = 18$, $p < 0.01$). Sexual behaviours were significantly positively correlated with aggressive behaviours ($r = 0.793$, $n = 18$, $p < 0.001$) and with marking behaviours ($r = 0.751$, $n = 18$, $p < 0.001$).

From observations recorded in 15 groups, 12 cases of multiple mounts (one female engaged in sexual behaviour with more than one male) were observed, including 9 attempts at mounts and 2 effective copulations that occurred during the first or the second day of oestrus. Typical mate-guarding behaviour was observed in 11 groups out of 15. This behaviour was performed only by the α males and occurred strictly on the first day of oestrus. High-ranking males remained close to the female and chased all the males that attempted to approach her. The mate-guarding behaviour seemed to be directed towards young females, since the number of breeding seasons experienced by non-monopolised females was significantly higher than that experienced by the monopolised females (4.3 ± 0.6 , $n = 9$, and 2.7 ± 0.3 , $n = 21$, respectively, $F_{1,28} = 5.0$, $p < 0.05$).

Role of the Females in the Sexual Competition between Males

No sexual behaviours and very few agonistic activities were observed in males before the introduction of sexually receptive females. Male behaviours completely and immediately changed when a female was introduced into the group and they significantly increased in frequency (marking: $MW = 4$, $n = 18$, $p < 0.001$; agonistic behaviours: $MW = 24$, $n = 18$, $p < 0.001$) (fig. 4).

The females' attacks on males were positively correlated with the number of aggressive interactions between males, and the frequency of their marking behaviours within a group ($r = 0.654$, $p < 0.01$ and $r = 0.568$, $p < 0.05$, $n = 18$, respectively). This indicates a stimulating role of females on male behavioural competition. Although aggressive behaviours of females were correlated with male sexual solicitations, α males received proportionally fewer attacks from females. The female response per male solicitation averaged 0.54 ± 0.04 for α males compared to 3.2 ± 0.8 and 2.7 ± 0.5 for β and γ males, respectively ($F_{2, 15} = 6.2$, $p < 0.01$). This could be related to the fact that most of the sexual solicitations by subordinate males were observed outside the period of peak vaginal swelling.

Relationships between Rank and Reproductive Success

Genetic determination of paternity using random amplified polymorphic DNA or microsatellites showed that 25 litters (49 infants) out of 27 (55 infants) were sired by the α male of the group. One litter of 3 babies was sired by the γ male. In this group, the dominance index of the α male was low (0.29) due to frequent attacks by the β male. Due to the intense competition between α and β males to reach dominance, the γ male had the opportunity to copulate with 1 female. Lastly, 1 case of multiple paternity was found for 1 litter of 3 infants, with 2 babies fathered by the α male and 1 by the β male.

According to the sperm competition hypothesis, for 3 males grouped with a female, the probability for a given male siring a litter or a baby is $1/3$, i.e. in our study, an expected frequency of 55/3 babies or 27/3 litters. Observed frequencies of paternity were significantly different: 51/55 for α males, 1/55 for β males and 3/55 for γ males ($\chi^2 = 87.5$, d.f. = 2, $p < 0.001$). This significant difference was maintained when using the number of litters instead of the number of babies. This is strong evidence that the high-ranking male in each group succeeded in monopolising oestrous females.

Discussion

Preliminary evidence obtained during this study suggests that the grey mouse lemur exhibits a mating system based on scramble competition polygyny. Male and female home ranges overlap, suggesting that both sexes may encounter multiple sexual partners [Fietz, 1999; Radespiel et al., 2001, 2002; Eberle and Kappeler, 2002]. Because intrasexual competition within polygynous males leads to sexual dimorphism [Mitani et al., 1996b], males of species lacking sexual dimorphism should not be expected to compete for females directly. The short breeding season and the high oestrus synchrony are strong indicators of the inability of males to monopolise access to oestrous females. The relatively great testicular development during the mating season in mouse lemurs suggests the presence of sperm competition, in which all the males have access to females and females do not exert any choice of their sexual partner [Kappeler, 1997a; Fietz, 1999; Atsalis, 2000; Schwab, 2000; Radespiel et al., 2001, 2002; Eberle and Kappeler, 2002].

However, no relationship has been found between mating systems and sexual dimorphism in strepsirhine primates [Jenkins and Albrecht, 1991; Lindenfors and Tullberg, 1998]. Moreover, arboreal and insectivorous species are, on average,

less dimorphic than terrestrial and frugivorous species [Plavcan and van Schaik, 1997]. Likewise, the mating season of the grey mouse lemur is very short, occurring over a 4-week period with several females entering oestrus in a given week [Eberle and Kappeler, 2002]. In such a situation, selection may have led to the evolution of relatively large testes, because males must produce sufficient spermatozoa within a relatively short period of time, rather than because of sperm competition [Ginsberg and Huck, 1989; Bercovitch and Nürnberg, 1996; Harcourt, 1996; Dixson, 1998].

Under our specific conditions of captivity, when male mouse lemurs are grouped in the presence of oestrous females, intense direct sexual competition develops between males. Dominant males showed the highest frequency of marking and sociosexual behaviours. A robust positive relationship between dominance and reproductive success was demonstrated by genetic paternity determinations. These results are compatible with the model of priority of access to oestrous females, in which male rank is reliably correlated with reproductive success [Cowlishaw and Dunbar, 1991; Bulger, 1993; de Ruiter and van Hooff, 1993; Altmann et al., 1996; Bercovitch and Nürnberg, 1996].

Both intermale competition for mates and female choice of mating partners may shape mating systems. Females can accept or solicit copulations with some males while refusing other males with aggressive behaviours [Pereira and Weiss, 1991; Perloe, 1992; Morland, 1993; Manson, 1995; Soltis et al., 1997]. In this study, we have demonstrated the important role of the females in the sexual competition between males. Their presence enhances the agonistic activity of the males and leads to the establishment of a strict hierarchy and to the emergence of a dominant male. Younger females, which are less sexually experienced, seem to be more monopolisable than older females. Younger females also exhibit higher levels of urinary oestrogen than older females do [Perret, in preparation]. They are more attractive to the males and are monopolisable because of their sexual inexperience. The older and more sexually experienced females seem to exert greater choice of their sexual partner, indicated by the fact that they are more aggressive towards subordinate males. Before becoming receptive, the females are highly aggressive towards male sexual solicitations. Female aggression would permit only the strongest males to copulate [Foerg, 1982a, b; Richard, 1992; Morland, 1993].

Chemical analysis of male urine reveals differential qualitative composition between the urine of dominant males and that of subordinate males [Schilling and Perret, 1987]. Using mass spectrography, the urine of dominant males contains a particular protein peak that increases when males are in the presence of females [Andrès et al., in preparation]. Moreover, at the beginning of the breeding season, males who will achieve a dominant position during sexual competition possess the best immune system [unpubl. data]. Although less attention has been given to olfactory signals, they could represent 'honest' signals allowing sexual choice, and it is likely that females perceive these differences and use them for mate choice [Ziegler et al., 1993; Kappeler, 1998; Smith and Abbott, 1998; Washabaugh and Snowdon, 1998]. In mouse lemurs, female mate choice has received little attention and can be more important than male social relationships in determining male mating success.

These results were obtained under captive conditions in which dominant males were able to control both receptive females and their male competitors. In field conditions, the number of interacting males is presumably higher and the typical guard-

ing behaviour displayed by high-ranking males would be less widespread. However, direct observations of wild mouse lemurs indicate a high number of agonistic interactions between males [Petter et al., 1977; Pagès-Feuillade, 1988], and temporary mate guarding has also been reported [Fietz, 1999; Eberle, pers. commun.].

However, even in captive conditions, where precopulatory competition between males occurred, 1 case of multiple paternity has been observed, as also reported by Radespiel et al. [2002], supporting the presence of sperm competition. This indicates that, in this opportunistic species, alternative mating strategies may coexist, depending on the availability and distribution of receptive females, which in turn depend on the availability and distribution of risks and resources in their environment.

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