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Mouse lemurs in space and time: a test of the socioecological model

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Abstract Socioecological theory predicts that the distribution of fertile females in space and time is the major determinant of male spacing behavior and mating strategies. Using a small nocturnal Malagasy primate, the gray mouse lemur (*Microcebus murinus*), we determined the spatiotemporal distribution of estrous females during the brief annual mating season to examine the predictive power of the socioecological model for male mating strategies. Mouse lemurs are particularly interesting in this respect because this polygynous species is characterized by seasonal reproduction, seasonally reversed sexual dimorphism, and relatively large testes. All resident animals in our 8-ha study area, a total of 30 adult males and 27 adult females, were individually marked and regularly recaptured to determine female reproductive status and to obtain home range data. We found that the mating season is limited to 4 weeks following female emergence from hibernation. Only 3–9 females could have synchronized estruses during a given week, indicating a moderately high male monopolization potential. However, receptive females were not spatially clumped and male ranges overlapped with those of many other rivals. Therefore, we suggest that individual powerful males may be unable to defend exclusive permanent access to receptive females because of prohibitive costs of range defense resulting from the strongly male-biased operational sex ratio and the corresponding intruder pressure. Our general conclusions are (1) that the socioecological model provides a useful heuristic framework for the study of mating systems, but that (2) it does not specify the degree of spatiotemporal clumping of receptive females at which male mating strategies switch among mate guarding, spatial exclusion of rivals, and roaming, and that (3) the operational sex ratio can have profound effects on male mating strategies as well.

Keywords Socioecology · Mating strategy · Sex ratio · Polygyny · *Microcebus*

Introduction

The socioecological model provides the main theoretical framework for the study of animal social and mating systems (Crook 1964; Emlen and Oring 1977). One of its primary goals is to link ecological and social factors in functional explanations of the distribution and association pattern of adult males and females in different taxa. Previous studies have confirmed one of the main assumptions of the model, i.e. that the distribution of females is primarily determined by the distribution of risks and resources in the environment (Jarman 1974; Davies 1991; Sterck et al. 1997). In addition, recent work has suggested that the threat of sexual coercion by males may also explain part of females' social strategies (Smuts and Smuts 1993; Clutton-Brock and Parker 1995).

The second main assumption of the socioecological model is that in mammals and other taxa where males have higher potential reproductive rates than females, males are expected to compete among themselves over access to fertile females and, thus, to tune their spacing and mating strategies closely to the distribution of these females (Clutton-Brock 1989; Clutton-Brock and Parker 1992). Male mating strategies, in turn, have far-reaching consequences for their behavior, physiology, and morphology. For example, if females are spatially clumped and their receptive periods are not synchronized, males have the highest potential to monopolize access to these females. Under these conditions, individual males with superior competitive abilities should be able to defend access to females (mate guarding) or their ranges (spatial exclusion) against rivals so that large body size and other determinants of male success in precopulatory competi-

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tion are favored by sexual selection (Ims 1988a; Clutton-Brock 1991; Weckerly 1998). If, on the other hand, females are dispersed in space and their fertile periods are highly synchronized in time, the potential to monopolize several females is much lower and males should roam widely to increase their encounter rates with fertile females (Ims 1988a, 1988b; Schwagmeyer 1988; Whitehead 1990). Large testis size and other adaptations to sperm competition are typically favored in this situation. Alternatively, males may opt to become monogamous under this situation and another combination of traits will ensue (Geffen et al. 1996; Brotherton and Manser 1997; FitzGibbon 1997). Other combinations of female distribution in space and time result in intermediate strengths of male monopolization potential, which is modulated by female choice and female reproductive interests under all conditions (e.g., Bercovitch 1995; Chism and Rogers 1997; Drickamer et al. 2000).

Just exactly how clumped or how synchronized receptive females have to be in order to elicit qualitative changes in male mating strategies remains poorly understood (Sandell and Liberg 1992; Dunbar 2000). Primates have provided valuable examples in earlier attempts to illuminate the ecological and social bases of male mating strategies because this small order exhibits a stunning diversity of social and mating systems (Crook and Gartlan 1966; Eisenberg et al. 1972; Clutton-Brock and Harvey 1977). More specifically, several independent taxa feature the two basic social situations of either solitary or gregarious females (Kappeler and van Schaik, in press), so that controlled comparisons among taxa can provide insights into the specific factors underlying male mating strategies (Gittleman 1989). The factors that determine whether groups of females can be monopolized by one male or whether they are associated with several males have been extensively investigated since the early days of socioecology (Ridley 1986; Altmann 1990; Kappeler 2000a). Recent analyses have demonstrated that both the absolute number of females and the probability that they have synchronized estruses have independent effects on male monopolization potential (Mitani et al. 1996; Nunn 1999; Dunbar 2000).

The mating strategies of primates with solitary females, a situation also characterizing the majority of other mammals, remain poorly understood, however. In some species with territorial (i.e., spatially dispersed) females that do not synchronize their cycles, males are permanently associated with only one female, even though their ranges could plausibly encompass those of several females (e.g., gibbons, *Hylobates* sp.; titi monkeys, *Callicebus* sp.), whereas males in other species (e.g., orangutans, *Pongo* sp.; pottos, *Perodicticus* sp.) with solitary females whose ranges overlap defend ranges that provide them with access to several females (Charles-Dominique 1977; Wright 1986; van Schaik and Dunbar 1990; van Schaik 1999). In further contrast, species with solitary females and a brief mating season (i.e., a high potential for estrous synchrony) can exhibit radically different mating strategies, as for example two species of dwarf lemurs studied in the same forest (*Cheirogaleus medius*: monogamy, Fietz 1999a; *Mirza coquereli*: scramble competition polygyny, Kappeler 1997a).

Studies of solitary Malagasy primates may be especially rewarding for attempts at understanding the determinants and consequences of male mating strategies because they include closely related taxa with variability in the spatiotemporal distribution of estrous females, degree of sexual dimorphism, and relative testis size (Kappeler 1997b). Mouse lemurs (*Microcebus* sp.) are small (30–100 g) nocturnal omnivores, and the most abundant solitary lemurs (Martin 1973). They occur in virtually all remaining Malagasy forests and therefore have great potential for illuminating the effects of variable ecological conditions on social systems.

Gray mouse lemurs (*Microcebus murinus*) spend the day in nests or tree holes in unisexual groups of variable size. Because they spend the majority of their nocturnal activity foraging alone, they are classified as a solitary species (Kappeler and van Schaik, in press). They have been reported to live in population nuclei consisting of several females with overlapping ranges and a few dominant males, surrounded by subordinate males (Martin 1973). At other sites, short-term studies suggested that adults are distributed more evenly and that ranges of multiple males and females overlap (Pagès-Feuillade 1988; Fietz 1999b). Mating takes place at night. In captivity, only a few males mate and they also have larger testes than their rivals, whose reproductive activity they can inhibit via urinary pheromones (Perret 1992). In the wild, however, no morphological evidence for two classes of males could be found (Schmid and Kappeler 1998). In addition, *M. murinus* is unique among primates in that females are on average larger and heavier than males, but sexual dimorphism in body mass fluctuates across the annual cycle, presumably as a result of a unique sex difference in life histories: only females hibernate for up to several months just prior to the annual mating season (Schmid and Kappeler 1998).

To resolve some of these partly contradictory observations about male spacing and mating strategies and to test predictions of the socioecological model for the underlying female distribution, we determined the spatial and temporal distribution of estrous females and related it to the distribution of males. Specifically, we tested the prediction that receptive females should be dispersed in space and or synchronized in time (Ims 1988a) if males engage in scramble competition polygyny, as suggested by indirect morphological evidence and preliminary observations (Kappeler 1997c; Fietz 1998).

Methods

We studied gray mouse lemurs (*M. murinus*) in Kirindy Forest, western Madagascar (Ganzhorn and Sorg 1996). Members of this population have been regularly captured and individually marked with transponders since 1994 within an 8-ha study area equipped with a rectangular system of foot trails at 25-m intervals (Schmid and Kappeler 1998). We baited Sherman live traps with banana and set them near trail intersections for three consecutive nights per month between September and December 1997, and additionally once per week between mid-October and mid-November. Captured animals were collected in the early morning, individually marked (or identified during recaptures) and released at the site of capture in the late afternoon. To minimize interference with the animal's nocturnal mating activities, most traps were checked in the early hours of the night in October and November so that no animal was detained for more than a few hours. A total of 27 females and 30 males were captured during this study. Comparison with long-term population records indicated that this sample included all adult residents present at the time.

We used coordinates of the intersections where animals were caught, together with coordinates of sleeping trees, identified by locating radio-collared animals during the day, to determine the location of individual home ranges. Each home range contained on average eight sleeping trees and 30–50 trapping stations. Because an earlier radio-tracking study in the same population yielded more precise estimates of the size of male and female home ranges, we calculated the center of activity for each individual and fitted a circular home range of mean size (females 1.3 ha, males 1.9 ha; P.M. Kappeler, unpublished data) around it. We preferred to use these mean estimates because they are more conservative in estimating home range overlap and, thus, the intensity of competition.

The reproductive state of females was determined by cytology of vaginal smears and external examination of vulval morphology. The vulva of mouse lemurs is sealed off with a membrane during most of the year (Petter-Rousseaux 1964). It opens only briefly during estrus and when birthing. In addition, the vulval area is flat and inconspicuous. During the early estrous cycle, the vulva reddens and begins to swell up for 5–15 days. Eventually, the closing membrane ruptures and the vulva remains open for an average of 6 days during which a female is receptive for only a few hours, typically during one of the first 3 days of vulval opening. Soon afterwards, the vulval area collapses and the vulva starts to reseal, showing a characteristic scar several days following estrus (Glatston 1979). Our field observations confirmed the sequence and duration of these phases of estrous cycles. The likely days of estrus were reconstructed using the assessment of female reproductive status on the days of capture. Vaginal smears were taken from some open females to examine characteristic cytological changes accompanying the phases of an estrous cycle (Glatston 1979; Izard and Rasmussen 1985) in a few equivocal cases.

This method allowed us to define the week of estrus of 22 of a total of 27 females known to be present, without unduly interrupting their mating activities. This reconstruction was not possible for the remaining 5 females because they were not captured at a state of vulval morphology that allowed us to determine their reproductive status. Because we wanted to include all resident females in our simulations, we assumed that the estruses of these five females were distributed in the same proportion across the weeks of the mating season as those of all other females. It should be noted that receptivity is limited to a few hours during a single night during these weeks (Glatston 1979) and that this estrous day could not be determined exactly. The degree of estrous synchrony was therefore difficult to determine precisely. For example, the females which experienced their estrus during the same week were possibly all receptive in the same night or, at the other extreme, their estruses were completely asynchronized.

To quantify the degree of reproductive synchrony, we divided the mating season into four 1-week periods based on our weekly trapping data (see below). Combinatory calculations were carried out to obtain exact probabilities for the observed temporal distributions of open females over the entire mating season, using the multinomial formula:

$$p(<n_1,\ldots,n_k>) = \left(\frac{k!}{l(s_1)!\ldots l(s_i)!}\right) \cdot \left(\frac{N!}{n_1!\ldots n_k!}\right)\left(\frac{1}{k}\right)^N$$

where N is the total number of individuals, n_1,..., n_k are the number of individuals in each of k groups (a group here refers to all females in estrus during the same week) and the term $l(s_i)$ refers to the number of groups with the same number of individuals. For example, the distribution <6,6,4,11> of 27 receptive females over four groups (here: weeks) contains three different group sizes, $s_1=6$, $s_2=4$ and $s_3=11$ with $l(s_1)=2$ and $l(s_2)=l(s_3)=1$ group(s). To determine the statistical significance of the observed degree of estrous synchrony, the probability for the observed temporal distribution of open females was compared with the probability of both the most even and the most probable distribution, which are the two possibilities to define maximal asynchrony (for details see Schank 1997).

To analyze the spatial distribution of estrous females we calculated Rasmussen's range-use index (RU; Rasmussen 1980). This square-based index was chosen because it considers variation in intensity with which different squares are used, as well as variation in grain. Moreover, it is neither affected by the number of squares over which it is calculated, nor by the sum of values in all squares. Furthermore, it can be used to compare simulated distributions with empirical distribution data and it can help to identify an order among several distributions from over-dispersed to random to clumped. It calculates all pair-wise sums of occupation status among all squares and weighs them according to the distance of the squares under consideration:

$$\mathrm{RU} = \frac{\left[\sum_{i=1}^{P}\left(X_i-\overline{X}\right)^2/P\right]^{1/2}}{\overline{X}}$$

where X_i=the sum of values in the ith pair of squares divided by the distance between their centers, and P=the total number of possible pairs of squares (for details see Rasmussen 1980).

After dividing the study area in 84 25×25 m squares, we determined each female's center of activity and assigned it to the corresponding square. Because of the large number of theoretically possible distributions, we related the observed value for a given number of females to a range of values obtained by simulating one million random distributions of the same number of females. Maximum clumping and even dispersion correspond to maximum and minimum values, respectively; random distributions yield intermediate values. In addition we used nearest-neighbor analysis (Hooge et al. 1999) for those females with an adequate number of neighbors (in our case only possible for week 4). Because we included the five females with unknown estrous dates, we had to calculate several observed values in both types of analyses to account for all possible combinations between "known" and "unknown" females. Below, we present the range of these values. These analyses provided a first estimate of the number of receptive females a given male gray mouse lemur could find within his home range.

Results

In September, only a few females were captured because most of them were still hibernating, whereas all males were already captured. Females emerged from hibernation in late September and open females were captured exclusively between mid-October and mid-November, resulting in a mating season of about 4 weeks (Fig. 1). The reconstruction of the temporal distribution of the likely estrous days of individual females is depicted in Fig. 2. The temporal distribution of receptive females was characterized by pronounced seasonality, but we found no evidence for significant synchrony. The probability of the temporal distribution of receptive periods among all females did not differ significantly from the

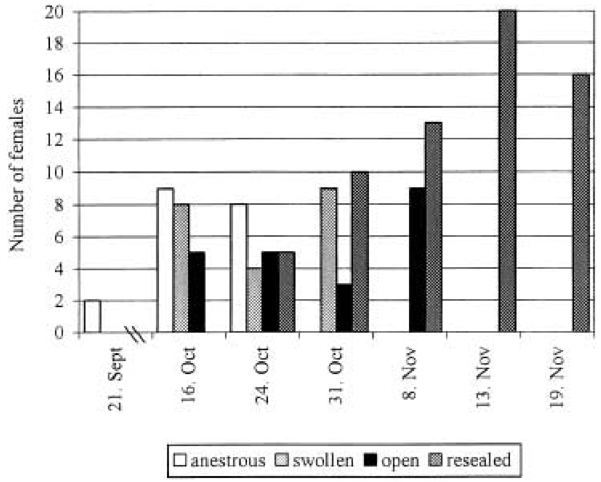

Fig. 1 Temporal distribution of females in different estrous states. At each trapping date, the estrous state of a subsample of 27 resident females was examined

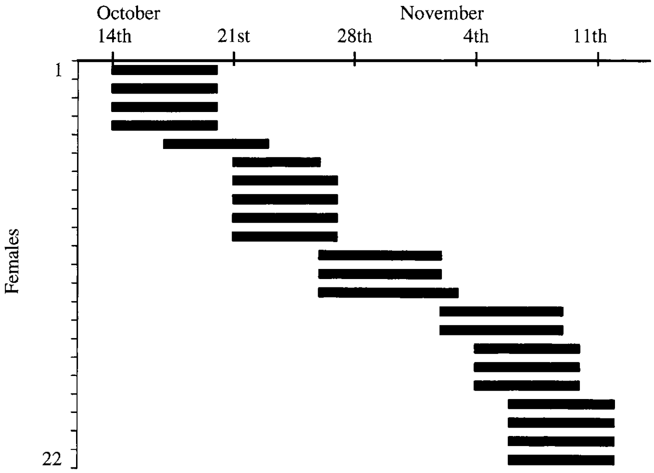

Fig. 2 Temporal distribution of open females. Each *bar* represents 1 of 22 females, whose dates of vulval opening are known. The horizontal position and the length of each bar indicate the estimated period and duration, respectively, of vulval opening. The females were divided into four groups according to the 4 weeks of mating season containing 5, 5, 3, and 9 individuals. To include all 27 resident females, we assumed that the estruses of the remaining 5 females were distributed in the same proportion across the weeks of the mating season as those of all other females, yielding 6, 6, 4, and 11 individuals

probability of the most even (7,7,7,6; P=0.56) or of the most probable (9,7,6,5; P=0.16) distribution, which are the two possibilities to define maximal asynchrony. Thus, considering only the observed temporal distribution of receptive females, a moderate to high male monopolization potential should be expected.

The spatial distribution of females in the study area was characterized by a high degree of range overlap (Fig. 3a). During the mating season, female home ranges overlapped with those of 1–15 other females (median: 10) and 2–18 males (median: 10). As a result, the number of receptive females within a given male's home range was determined to have varied between 1 and 9 per week (median: 4). Furthermore, during each of the 4 weeks of the mating season, the spatial distribution of open females was random or exhibited a tendency toward an even distribution (Table 1, Fig. 4). The results of the nearest-neighbor analysis for week 4 (R=1.21–1.37, $|z|$=1.31–2.36, P<0.05) also corresponded to values for random or even distributions. Thus, estrous females were not clumped in space, resulting in a low to moderate male monopolization potential.

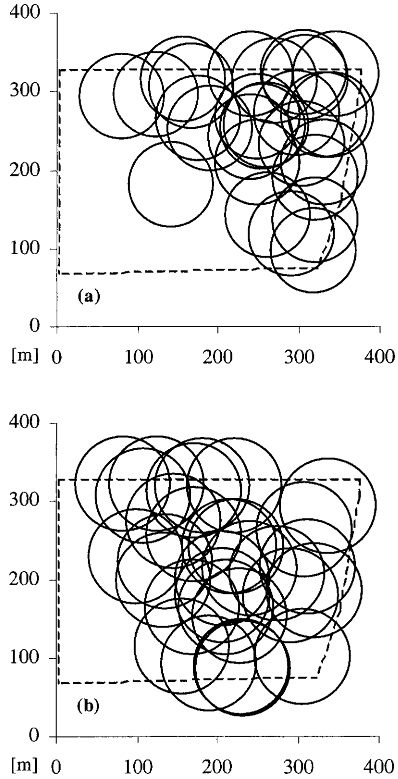

Fig. 3 Spatial distribution of 27 females (**a**) and 30 males (**b**). Each *circle* represents the estimated home range of one animal, centered around its calculated center of activity during the study period. The *dashed line* indicates the borders of the trapping area

Male home ranges also overlapped with those of many rivals (4–19, median: 11; Fig. 3b), providing no evidence for spatial exclusion and, thus, male monopolization of females in this way. Moreover, during opportunistic direct observations of estrous females, several males were observed in their vicinity or even attempting to mate. Some males succeeded in temporarily monopolizing individual females by aggressive mate guarding, but all females eventually mated with more than one male. Finally, we note that during each week of the mating season, the operational sex ratio (OSR) was heavily biased toward males. Our conservative estimates indicate that up to 18 males may have competed for a given female per night, and the OSR could have been even more strongly male-biased toward the end of the mating season as the number of already mated females increased. The adult sex ratio of this population has been even or

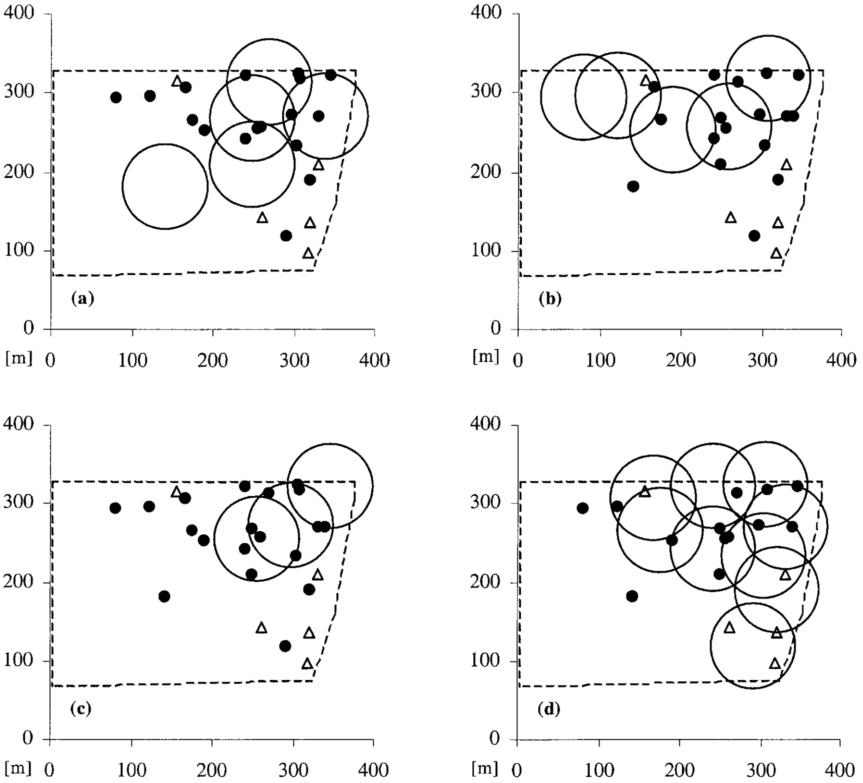

Fig. 4 Spatial and temporal distribution of receptive females. *Circles* indicate home ranges of females which were receptive during weeks 1–4 (**a–d**). *Dots* indicates centers of activity of non-receptive females. *Triangles* represent five females, whose week of receptivity remained unknown. The *dashed line* indicates the borders of the trapping area

Table 1 Spatial distribution of estrous females. For each of the 4 weeks of the mating season, we calculated expected minimal (*Min*), mean and maximal (*Max*) RU indices for the given number of estrous females, using 1,000,000 simulations. *Min* corresponds to an even distribution, *Max* to a clumped distribution, and *Mean* to a random distribution. We present a range of observed values because we also included five females whose estrous dates remained unknown

Week	Number of estrous females	Min RU	Mean RU	Max RU	Observed values
1	6	3.08	3.31	4.77	3.13–3.16
2	6	3.08	3.31	4.77	3.30–3.31
3	4	3.55	4.02	6.38	4.04–4.09
4	11	2.26	2.49	3.66	2.20–2.22

slightly male-biased from the beginning of our study (P.M. Kappeler and M. Eberle, unpublished data).

Discussion

The most important results of our study revealed that receptive gray mouse lemur females were not clumped in space and time. Below, we discuss potential causes and consequences of this distribution for male mating strategies and explore its theoretical implications.

Female distribution

The spatial distribution of female gray mouse lemurs appears to be mainly determined by environmental conditions. While hibernating during the dry season, they share tree holes with several other females. Particular trees and group sizes confer substantial energy savings (Perret 1998; Radespiel et al. 1998; Schmid 1998a) and their limited distribution results in a highly clumped spatial distribution of females during the austral winter. Males are active throughout this period (Schmid 1998b; Schmid and Kappeler 1998) and inspect or even join tree holes used by females. This may provide them with information about the approximate location and number of potential mates later on, but at the time of female inactivity, and thus sexual quiescence, it has apparently no immediate consequences for their mating strategies. However, whether dominant males studied by Martin (1973) were able to defend access to clumped females against peripheral males because sleeping sites in this particular habitat in southern Madagascar were extremely limited remains to be examined.

Following emergence from hibernation, females are more widely dispersed during their activity period because of their solitary nocturnal foraging, but continue to share daytime sleeping sites, albeit with fewer females (Schmid 1997), so that they are distributed in more, but smaller sleeping groups. Solitary foraging may be necessitated by the nature of important food sources, such as arthropod prey and gum sites, which cannot be exploited simultaneously by several animals (Kappeler 1997b). As a result, there is little potential for effective resource defense or defense of several females by males.

Male distribution

The spatial distribution of *M. murinus* males revealed no evidence for permanent or temporal territoriality. Male home ranges overlapped with those of several other males. There was also no evidence for the existence of physically powerful males that defended access to a core of several females against weaker rivals (see Schmid and Kappeler 1998). During the mating season, males mostly sleep alone, but they also occasionally share tree holes with up to four other, usually closely related males (M. Eberle, unpublished data; Radespiel et al. 1998; Schmid 1998a). Thus, males apparently exclude each other from sleeping sites, but they tolerate a high degree of overlap of their ranges of activity. This may result from the high density of males, which could make intruder pressure and, thus, costs of range defense too high. The only adjustment of male spacing behavior in response to the presence of receptive females was a temporary increase in home range area (P.M. Kappeler, unpublished data; Fietz 1999a). This has also been observed in other populations of gray mouse lemurs (Radespiel 2000), in closely related lemur species (Kappeler 1997a), and in other mammals, such as thirteen-lined ground squirrels (*Spermophilus tridecemlineatus*). In the latter case, males with larger home ranges during the mating season than other males were found to also have above-average mating success (Schwagmeyer 1988).

The temporary character of male home range extensions indicates that this strategy may be limited by energetic costs. Indeed, *M. murinus* male body mass decreased significantly during the 4-week mating season, whereas females were able to put on weight during the same period (M. Eberle, unpublished data; Schmid 1998b). Similarly, in Richardson’s ground squirrels (*S. richardsonii*), males had higher energetic and survival costs than females during the brief mating season (Michener and McLean 1996; Michener 1998). Thus, permanent territoriality or maintenance of larger ranges appears to be energetically too expensive, favoring the combination of range overlap and roaming.

Reproductive synchrony

Reproductive activity in the Kirindy mouse lemur population is highly seasonal but not significantly synchronized (see also Pereira 1991). The observed temporal distribution of estrous females in this population provides another example for the importance of a distinction between reproductive seasonality and synchrony (see Pereira et al. 2000). Our study also underlines previously noted difficulties quantifying the degree of synchrony with imperfect information (Rhine 1995, 1999; Schank 1997), even though we estimated the distribution of receptive periods with a level of detail unmatched by previous studies of solitary primates (see also Stockley 1996).

Furthermore, our analyses generate questions about the biological significance of synchrony that impact on its operational definition. Specifically, the meaning of synchrony always critically depends on which female reproductive states males are able to discriminate. If females are only attractive during the state of receptivity (Beach 1976), the degree of synchrony can be quantified as we did here. However, if females attract males during the entire period of vulval opening, this would result in increased temporal synchrony from the males’ perspective, and, thus, a rapidly decreasing monopolization potential. Controlled choice experiments with captive animals may reveal more about males’ ability to detect estrus (e.g., Clark 1982).

Male reproductive strategies

The probability of the temporal distribution of female receptive periods differed significantly neither from the probability of the most even nor of the most probable distribution, which are the two possibilities to define maximal asynchrony. Thus, each female could, in principle, be monopolized by a powerful male with which she shares part of her home range, assuming that males are able to predict the occurrence of receptive females in space and time, and that they are able to guard them. In this context, it is important to note that male monopolization can take at least two forms: (permanent) spatial exclusion of rivals or temporal mate guarding. The potential for both types of monopolization is influenced by female interests and the OSR (Emlen and Oring 1977; Lifjeld et al. 1994; Chism and Rogers 1997; Clutton-Brock et al. 1997; Kempenaers 1997). Little is yet known about female mate choice in mouse lemurs, but preliminary results of controlled mating experiments with captive animals indicate that females accept all males during peak estrus (M. Eberle, unpublished data) and, thus, apparently exercise little choice and leave sufficient opportunities for male monopolization.

The OSR in our population was highly male-biased: the ranges of estrous females overlapped with those of up to 18 males. Furthermore, as the number of already mated females increases over the course of the reproductive season, the OSR should become increasingly male-biased, which, in turn, may lead to changes in male competitive strategies. This potential effect will have to be examined in a future study focusing specifically on this aspect of male behavior. In several ground squirrel species with roving males, the OSR also ranged on average between 10 and 20 males per female, increasing as the number of already mated females within a male's home range increased, and was much higher than in other closely related species with other forms of male competition (Schwagmeyer and Woonter 1985; Sherman 1989; Michener and McLean 1996; Waterman 1998). Thus, a high OSR does not necessarily result in more intense mate competition (cf. Emlen and Oring 1977), but may limit male monopolization potential because range or female defense are too costly.

Even or male-biased adult sex ratios are common among lemurs, but their adaptive value remains unknown (Kappeler 2000b). Studies in captivity demonstrated that mouse lemur females can manipulate birth sex ratios so that grouped females produce more sons (Perret 1990, 1996), and that maternal care is biased towards male neonates (Colas 1999). Females may over-invest in sons to reduce local resource competition with daughters (Clark 1978; Packer et al. 2000), but the dynamics and adaptive significance of the unusual sex ratio of this and other lemur populations remains to be studied in detail.

Conclusions and open questions

The results of our study indicate that information about either the spatial or temporal distribution of receptive females alone is insufficient to predict male behavior. As suggested by theoretical (e.g., Dunbar 2000) and some empirical analyses (Ims 1988a), at least these two aspects need to be considered simultaneously. Furthermore, the results of our study identified the OSR as an additional likely determinant of male mating strategies that interacts with female distribution. Thus, the original socioecological model is clearly heuristically valuable, but it fails to provide detailed predictions in this respect and it is therefore difficult to evaluate in practice. For example, even though the available behavioral and morphological evidence indicates that scramble competition polygyny is the predominant mating system of this mouse lemur population, we cannot exclude other mating strategies based on data on the animals' distribution alone, because specific switching points for male and female mating strategies are not predicted by the socioecological model.

Moreover, within polygyny, several mating strategies can coexist. In Richardson's ground squirrels (*S. richardsonii*), for example, the proportion of roaming and staying males varied according to female density (Davis and Murie 1985). This proportion can be also influenced by other factors, such as the length of estrus, dominance relations among males, or the degree of estrous synchrony (Sandell and Liberg 1992). Estrous length and synchrony, as well as female density and numbers, may, within ecological constraints, be manipulated by females, and all of them can affect male mating strategies (see e.g., Clutton-Brock et al. 1997; Watts 1998).

In conclusion, this study demonstrated that determinants of, and switching points for male mating strategies in species with solitary females are difficult to identify. We do not yet know whether male mating success is skewed, whether males change their mating strategies over the course of the reproductive season, whether males have the same information about female distribution as we do, or whether they have additional information not available to us. Moreover, whether factors external to this problem, such as infanticide risk or need for male parental care, affect female mate preferences, spacing behavior, or estrous timing remains to be determined. Spacing and mating experiments in which the number and distribution of females are systematically varied (e.g., Ims 1988a), direct observations of both sexes during the mating season, and genetic parenthood analysis should provide partial answers to these open questions.

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