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## FEMALE DOMINANCE IN COMPETITION FOR GUM TREES IN THE GREY MOUSE LEMUR *MICROCEBUS MURINUS*

Fabien GÉNIN<sup>1</sup>

### RÉSUMÉ

Chez les mammifères, les femelles sont généralement plus limitées par les ressources alimentaires que les mâles, du fait de leur plus grand investissement dans la reproduction. Dans une forêt sèche décidue de l'ouest de Madagascar, le poids corporel, la distribution spatiale, les comportements alimentaires et sociaux de Microcèbes gris (*Microcebus murinus*) ont été suivis pendant la période d'engraissement automnal (mars-avril) à l'aide de captures-recaptures d'animaux marqués et d'observations comportementales. Seuls quelques animaux (23 %) ont pris du poids et les femelles étaient en général plus lourdes que les mâles. La distribution spatiale des captures des animaux des deux sexes s'est superposée à celle des arbres à gomme, lesquels sont apparus comme une ressource-clef à cette période (75 % du régime). De plus, les femelles étaient d'autant plus lourdes qu'elles étaient capturées près des arbres à gomme, alors que cette corrélation n'a pas été retrouvée chez les mâles. Une exclusion spatiale des captures de mâles et de femelles a également été observée. En fait, une compétition locale pour les ressources, confirmée par les observations comportementales, semble expliquer le poids corporel élevé d'animaux dominants, c'est-à-dire en particulier des femelles. La mise en réserve de graisse corporelle pourrait affecter à la fois la survie à la saison sèche et le succès reproducteur à la saison des pluies suivante. Ainsi, la compétition alimentaire à l'automne pourrait avoir des conséquences importantes sur l'organisation socio-spatiale du Microcèbe gris en produisant une grande variabilité intra- et inter-sexuelle.

### SUMMARY

Due to their higher reproductive investment, female mammals are usually more dependent on food than males. In a dry deciduous forest of western Madagascar, body mass, spacing patterns, feeding and social behaviour of Grey Mouse Lemurs (Schmid & Kappeler, 1998) were investigated during the autumn fattening phase (March-April) using mark-recapture and behavioral observations. Only a few animals (23%) increased their body mass, and females were generally heavier than males. The spatial distribution of captures of both males and females followed the distribution of gum trees, which appeared as a keystone resource at this period (about 75% of the diet). Moreover, females trapped near gum trees were significantly heavier than others, whereas no such difference was observed in males. Spatial exclusion was noted between male and female capture locations. Local resource competition, confirmed by

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behavioural observations, may have led to higher body mass in dominant animals, and especially in females. Storage of fat may affect survival during the dry season and reproductive success at the ensuing rainy season. Therefore, feeding competition, by resulting in high inter- and intrasexual differences in fattening and use of space, may have implications for dynamics of populations and social organization.

## INTRODUCTION

Intraspecific competition and use of space depend on resource availability and capacity of animals to monopolize rare resources (Emlen & Oring, 1977). Within mammals, reproductive investment is usually much higher in females than in males (Trivers, 1972). Consequently, males and females often show strong differences in management of time and energy (Armitage, 1998; Michener, 1998). The FIS (Female In Space) hypothesis suggests that abundance, distribution and renewal rate of food determine the spacing pattern of females, whereas the spacing pattern of males is limited by access to receptive females (Wrangham, 1980; Van Schaik & Van Hooff, 1983; Ims, 1988; Ostfeld, 1990; Charles-Dominique, 1995; Koenig, 2002). However, access to food and attraction to females vary in time, and models must account for seasonality of reproduction and food availability (Ostfeld, 1990; Charles-Dominique, 1995). Mating competition disappears during reproductive inactivity and both sexes compete for food resources. In species that accumulate fat stores to survive the period of food shortage, feeding competition should be especially noticeable during the fattening phase. By contrast, during the ensuing period of food shortage, fat stores and decrease of food intake minimizing dependence of food, as well as other seasonal adaptations such as huddling behaviour and low activity are associated with reduced territoriality and aggressiveness (Stephenson & Racey, 1994).

Territoriality is usually defined by exclusiveness of home range (Ostfeld, 1990). However, patchily distributed resources can be defended locally. Local resource competition (LRC) between closely related females may explain the male-biased sex-ratio observed in a bushbaby, *Galago crassicaudatus* (Clark, 1978). This model should be applicable in various species in which females are kin-bonded and philopatric whereas males are more mobile. This type of social organization and variability in natal sex ratio have been reported in the Grey Mouse Lemur (*Microcebus murinus*), a small nocturnal lemur considered non-territorial (Radespiel, 2000; Eberle & Kappeler, 2002). In captive Grey Mouse Lemurs, grouped females have been shown to overproduce sons (Perret, 1990, 1996; Perret & Colas, 1997). Nothing is known about possible local resource defense in this species. Radio-tracking and capture-recapture studies revealed that home ranges overlap highly and are larger in males than in females (Barre *et al.*, 1988; Pagès, 1988; Radespiel, 2000; Eberle & Kappeler, 2002). Moreover, the size of male home range has been reported to change seasonally (Radespiel, 2000). In the natural habitat of western Madagascar, its breeding season is restricted to the summer months while the resources on which it feeds (fruits, flowers, new leaves, gums, insects) are abundant (Martin, 1972; Hladik, 1980; Hladik *et al.*, 1980; Barre *et al.*, 1988; Sorg & Rohner, 1996). By contrast, during the 6 months of cool and dry winter, both sexes enter a state of reproductive inactivity (Pagès, 1988; Schmid & Kappeler, 1998). They exhibit daily torpor and huddling behavior (Radespiel *et al.*, 1998; Schmid & Kappeler, 1998). In constant captive conditions, short photoperiod induces fatte-

ning by an increase of food intake and a decrease of locomotor activity with no marked sex-specific difference (Pagès & Petter-Rousseaux, 1980; Génin & Perret, 2000). In western Madagascar, fattening should occur within the month following the austral equinox corresponding to the short photoperiod induction (Hladik *et al.*, 1980; Schmid, 1999). In wild populations, autumn fattening has been noted essentially in females, and males remain active during the dry season (Hladik *et al.*, 1980; Schmid, 1999).

If gums comprise a major part of the diet, and since Grey Mouse Lemurs are sexually inactive during the dry season, 1) spatial distribution of animals of both genders should fit spatial distribution of gum trees, 2) a local competition for gum trees can be expected and should determine at least partially the spacing pattern of the animals, 3) the higher weight gain of females should be due to their dominance over males in feeding competition during the phase of hyperphagia, rather than physiological sex-specific differences. This study aimed to investigate feeding competition for gum trees, using behavioral observations and mark-recaptures. The spacing pattern of gum trees and the spacing pattern of male and female captures were compared in a wild population of Grey Mouse Lemurs in western Madagascar, during the pre-winter fattening period.

## METHODS

### STUDY SITE AND ANIMALS

This study was conducted in western Madagascar after the breeding season in March-April 1999 — austral autumn, corresponding to the expected pre-winter fattening period — in Kirindy Reserve, a dry deciduous forest concession of the Centre de Formation Professionnelle Forestière (CFPF), 60 km northeast of Morondava (20°03'S, 44°39'E). The study site is a 7.3 ha area where mouse lemurs have been studied since 1994 by the Deutsches Primatenzentrum (DPZ) research team (Schmid, 1999). Animals were individually marked by subcutaneous transponder (TROVAN®, Weilerswist, Germany). Animals were weighed with an electronic balance ( $\pm 1$  g). The lightest recognized adult weighted 45 g (Eberle, pers. com.). Thus, unknown animals were included in analyses if their body mass were above 45 g, assuming that juveniles of 45 g and more had reached adult size.

### TRAPPING

To trap these nocturnal, arboreal animals, 140 Sherman traps baited with banana were set 1-2 m above the ground at 25 m intervals along a trail system, 1-2 h before dusk and checked 1 h after dawn. To follow body mass after the austral equinox (short photoperiod) and to assess spatial distribution of animals, 3 trapping sessions of 2-3 successive nights were performed following the trapping protocol established by the DPZ research team (session 1 before the equinox – March 11, 13, and 14; session 2 after the equinox – March 30, 31, and April 1; and session 3 – April 30 and May 1). Captured animals were identified and their body masses measured. Animals were released at capture locations shortly before dusk (Schmid, 1999). To evaluate autumn fattening maximum body mass of each trapping session was compared across recap-

tures. Because trapping may affect body mass, first capture only was considered within each trapping session. To compare body mass of animals in the context of feeding competition, maximum body mass only was considered.

#### DISTRIBUTION OF GUM TREES

Minimum distance from the nearest gum tree was determined in all captures of the same individual. Trees exuding gum were identified and considered available gum trees if any animal was observed feeding on its gum exudate or gum from a conspecific tree (*Terminalia mantaliopsis*, *Terminalia bovinii*, Combretaceae; unidentified Meliaceae (2 species) and *Commiphora* sp., Burseraceae).

#### OBSERVATION PROCEDURE

To study feeding behavior and competition, 15 bouts of nocturnal census were conducted in the 3 h following dusk (total 24 h) or in the 3 h preceding dawn (total 21 h). All census walks covered the entire grid crossing each trap location only once and alternating between N-S trails and E-W trails. To minimize effects of time on activity rate, each walk started alternately in a different corner of the grid. Behaviour of visible mouse lemurs was observed for about 3 min each. Seventeen 30 min-focal observations were performed on a single gum tree (8 within the 3 h following dusk and 9 at different hours of the night). Animals were observed with a headlamp and binoculars (8X). For each observation bout, feeding activity (foraging, feeding) was recorded. Every food item was sampled when possible for identification. Direct interactions were also recorded (contact fight, chase, being chased as agonistic behaviours).

#### STATISTICAL ANALYSES

All values are means  $\pm$  SEM. Normality of distributions were evaluated by calculating the Skewness and the Kurtosis. A log-transformation was used in cases of non-normal distributions. 99.9% confidence interval was used to test the presence of outliers in distribution of male body masses. Pairwise comparisons were made using Student's t-test. A Mann-Whitney U-test was used for comparison of recaptures per individual. The number of different individuals trapped according to presence or absence of gum trees in a 25 m or a 10 m range and maximum body mass were compared using G-tests. Correlation between parameters was evaluated by linear regression analyses. Since captures were performed on a regular grid, correlations with the distance from nearest gum tree as well as correlations with number of captures were performed using the Spearman correlation coefficient  $r_s$ .

## RESULTS

#### AUTUMN FATTENING

Sixty two adult Grey Mouse Lemurs (26 males, 36 females) were trapped in 227 captures. Nine new animals of body mass below 45 g (3 males and 5 females) were trapped in 30 captures. The number of captures per individual showed no significant difference between males and females ( $U = 521.0$ , d.f. = 1,  $p = 0.44$ ).

Body mass changes between session 1 and session 2 were analysed in 12 males and 17 females (Fig. 1). Within about 2 weeks, female body mass decreased ( $F_{1,11} = 13.0$ ,  $p < 0.005$ ) while male body mass did not change significantly ( $F_{1,11} = 1.6$ ,  $p > 0.05$ ). Moreover, female body mass was significantly higher than male body mass ( $F_{1,27} = 11.2$ ,  $p < 0.005$ ). Between session 2 and session 3, 8 retrapped males and 9 retrapped females showed no significant change ( $F_{1,15} = 0.6$ ,  $p > 0.05$ ) and no sex specific difference in body mass ( $F_{1,15} = 0.1$ ,  $p > 0.05$ ). Only 4 males in 15 (27%) and 5 females in 24 (21%) had increased their body mass by session 3.

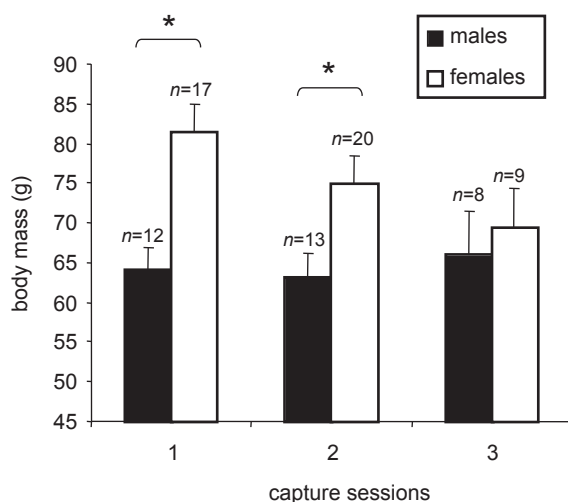


Figure 1. — Changes in body mass of male and female Grey Mouse Lemurs retrapped at least through 2 consecutive trapping sessions. Seasonal fattening was expected after the austral autumn equinox corresponding to the shift from long photoperiod to short photoperiod. Session 1 before the equinox – March 11, 13, and 14; session 2 after the equinox – March 30, 31, and April 1; and session 3 – April 30 and May 1.

Maximum body mass averaged  $63 \pm 2$  g in males ( $n = 26$ ) and  $72 \pm 3$  g in females ( $n = 36$ ). Seven females reached high body mass of more than 90 g. All these heavy females were at least 2 years old and one of them was at least 5 years old (Table I). One male reached 101 g which was significantly heavier than the other males, which averaged  $61 \text{ g} \pm 2$  sem (Studentized residual = 4.3,  $n = 26$ ,  $p < 0.001$ ). The heaviest females were trapped and retrapped more often than the lightest females: the number of captures was positively correlated with body mass ( $r_s = 0.514$ ,  $p < 0.001$ ,  $n = 36$ ). By contrast, no such significant correlation was found in male recaptures ( $r_s = 0.350$ ,  $p > 0.05$ ,  $n = 26$ ).

#### SPACING PATTERN AND GUM TREES

Thirty one gum trees occurred within the study area: 25 *Terminalia mantaliopsis*, 1 *Terminalia bovinii*, 4 unidentified Meliaceae and one injured *Commiphora* sp.

TABLE I

*Maximum body mass of males (♂) and females (♀) that reached 90 g and more, minimum distance to the nearest gum tree, and date of their first capture (communicated by Manfred Eberle). \* Females at least 5 years old trapped at the capture location where the maximum number of other individuals were found (see text)*

Sex	Maximum body mass (g)	Distance to the nearest gum tree	1 <sup>st</sup> capture
♀	90	0	1995
♀*	92	0	1994
♀	93	25	1998
♀	99	10	1995
♀	101	16	1997
♀	103	5	1996
♀	103	10	1996
♂	101	0	1996

The spatial distribution of adult captures was significantly linked to the spatial distribution of gum trees (Fig. 2). Most captures occurred at capture locations where a gum tree was found in a 25 m range ( $G = 10.3$ , d.f. = 1,  $p < 0.01$ ) with no significant difference between males and females ( $G = 1.1$ , d.f. = 1,  $p > 0.05$ ). By contrast, captures of juveniles were not significantly dependent of the presence of gum trees in a 25 m range ( $G = 0.5$ , d.f. = 1,  $p > 0.05$ ).

Animals were trapped in 87 out of 140 trapping locations. Animals trapped near gum trees were retrapped more often than animals trapped further from gum trees. The total number of captures per individual was negatively correlated with the minimum distance from the nearest gum tree ( $r_s = -0.300$ ,  $p < 0.02$ ,  $n = 62$ ).

Up to 6 different adults were trapped at the same trap location. The number of different individuals trapped at each capture location was negatively correlated to the distance of the nearest gum tree ( $r_s = -0.522$ ,  $p < 0.001$ ,  $n = 140$ ). At trap locations where at least one capture occurred, this correlation was found in captures of males, as well as in captures of females (respectively,  $r_s = -0.398$ ,  $p < 0.01$ ,  $n = 53$ ;  $r_s = -0.232$ ,  $p < 0.05$ ,  $n = 70$ ).

#### EXCLUSION BETWEEN MALES AND FEMALES

Further, a pattern of local spatial exclusion between males and females was found, especially far from gum trees (Fig. 2). Males and females were trapped at the same capture locations mainly where gum trees were found in a 25 m range (36 capture locations) whereas the 51 capture locations where only one gender was found, occurred mainly far from gum trees ( $G = 5.2$ , d.f. = 1,  $p < 0.05$ ). Females seemed

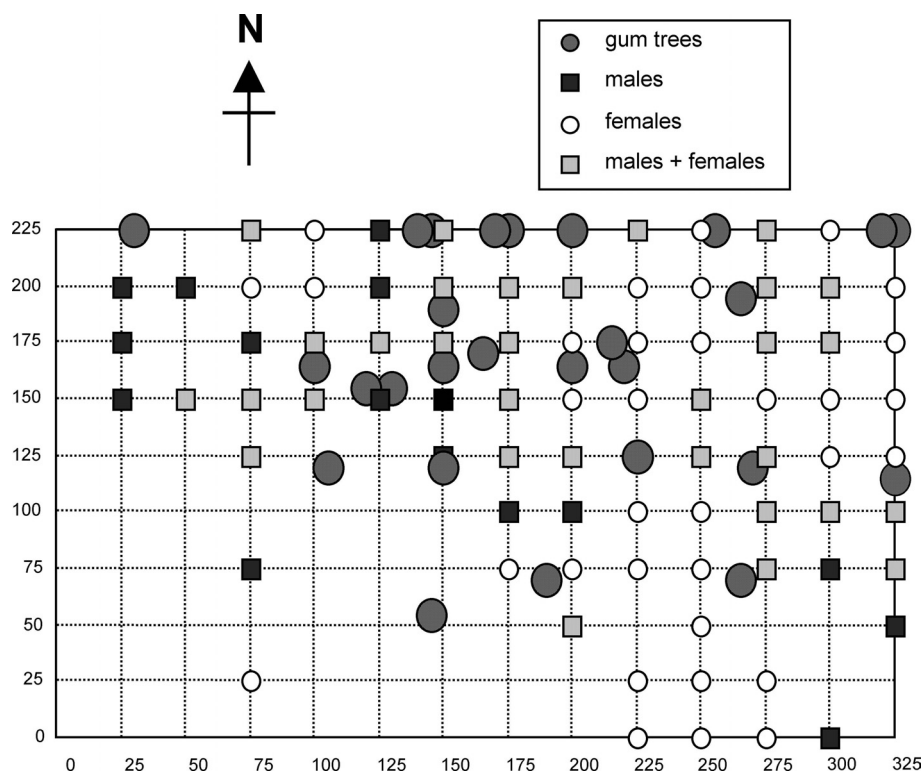


Figure 2. — Male and female captures at each trap location of the 8.75 ha grid (regular 25 m trail system) and spacing pattern of the 31 gum trees found in the study area. Capture locations of both males and females were indicated. The grid was edged by a track on its north side and by the Petit Kirindy river on its east side (dry at the end of the study).

to exclude males. Only males were trapped in 17 capture locations and only females were trapped in 34 capture locations. Fifteen males out of 26 (58%) were trapped at least once at capture locations where females were trapped (female-present location). Sixteen females out of 36 (44%) were trapped at least once at capture locations where males were trapped.

Males trapped at female-present locations were compared to males always trapped at male capture locations (Table II). Males sharing capture locations with females were mostly trapped where no gum tree was found in a 10 m range (12 out of 15). By contrast, males always trapped where no female was trapped were mostly found with gum trees in a 10 m range (8 out of 11) ( $G = 8.1$ ,  $d.f. = 1$ ,  $p < 0.01$ ).

#### BODY MASS AND DISTANCE TO GUM TREES

Females were significantly heavier when trapped near gum trees (Table I). Body mass of females was negatively correlated to the minimum distance of the nearest gum tree ( $r_s = -0.407$ ,  $p < 0.01$ ,  $n = 36$ ). No such significant correlation was

TABLE II

Number of male individuals that reached body mass above or below 66 g at capture locations where at least one gum tree was found in a 10 m range (gum) or not (no gum), and/or at capture locations where at least one female was trapped (with females) or not (without female). The chosen limit of 66 g corresponds to the median value of maximum body mass of all animals including females

	Maximum body mass	Gum trees < 10 m		Total
		gum	no gum	
With female	< 66 g	1	11	12
	≥ 66 g	2	1	3
		3	12	15
Without female	< 66 g	4	1	5
	≥ 66 g	4	2	6
		8	3	11
Total		11	15	26

observed in males ( $r_s = -0.218$ ,  $p > 0.05$ ,  $n = 26$ ). However, the heaviest males were all trapped at least once in a 10 m range of a gum tree (5 of 5 males with body mass above 70 g). The median of maximum body mass of all animals (66 g) was chosen as limit between light and heavy males. In males, the presence of females at capture locations and presence of gum trees in a 10 m range affected body mass, if the number of males that reached a maximum body mass above 66 g are compared with the number of males that remained below 66 g ( $G = 16.6$ , d.f. = 4,  $p < 0.01$ ; Table II). The number of males trapped where gum trees had been found in a 10 m range was higher if males did not share any capture location with females (8 out of 11) than if they did (3 out of 15) ( $G = 8.1$ , d.f. = 1,  $p < 0.01$ ). The number of heavy males (> 66 g) was higher where no female was trapped (6 out of 9) whereas light males (< 66 g) were mostly found where females were trapped (12 out of 17) ( $G = 8.1$ , d.f. = 1,  $p < 0.01$ ). Heavy males were mostly trapped where gum trees had been found in a 10 m range (6 out of 9) whereas light males were generally found far from gum trees (12 out of 17) ( $G = 4.0$ , d.f. = 1,  $p < 0.05$ ). The heaviest male (101 g) was trapped where females were trapped (2 out of 4) and where gum trees had been found in a 10 m range (2 out of 4).

#### FEEDING COMPETITION

Mouse lemurs were encountered 379 times during nocturnal censusing. Of the 144 foraging episodes observed, 106 involved gum-eating (75%), 8 fruit-eating (*Tacca leontopetaloides*, Taccaceae, in March; Cf. *Tarenna* sp., Rubiaceae, *Grewia trifolia*, Tiliaceae, from March to May) and 30 invertebrate-eating or hunting.

In thirty-four cases on 7 different gum trees, I observed one animal monopolize a gum tree with one or several other animals in close proximity (< 10 m from the gum tree). Fifty-nine out of 65 agonistic interactions (all chases) took place on the same gum trees.

A trap location with 2 nearby gum trees (*Terminalia mantaliopsis* and a *Melialea* sp. corresponding to the maximum of captures (7 captures of 5 different adults) was chosen for seventeen focal observations of 30 minutes. This tree was visited by one or several mouse lemurs shortly after dusk and afterward, by a Fork-marked Lemur *Phaner furcifer* (specialized-gummivorous Cheirogaleidae). The Fork-marked Lemur chased a mouse lemur 4 times in 4 different nights. Each chase was followed by a territorial call by the Fork-marked Lemur. Up to 5 different mouse lemurs were observed together in the gum trees. The oldest female trapped (92 g and at least 5 years old, Table I) was observed 6 times out of 17 focal observations. Each time she chased one or several other individuals but tolerated another individual. Thirteen times in 17, one to 3 individuals stayed near the tree while one or several others were foraging in it.

## DISCUSSION

Despite the weight gain of a few individuals of both genders, no significant autumn fattening was found in retrapped adult Grey Mouse Lemurs. However, a weight gain has been found in females in the same study area (Schmid, 1999). Likewise, in the nearby Marosalaza forest, fattening occurred in both genders, but was less pronounced in males from March to May (Hladik *et al.*, 1980). Food availability (fruits, flowers and new leaves) increased from March to April at Marosalaza whereas fruiting trees were scarce in April in the Kirindy forest (Hladik, 1980; Sorg & Rohner, 1996). The related Fat-tailed Dwarf Lemur *Cheirogaleus medius* showed an increase in fruit eating during the pre-hibernation phase (Fietz & Ganzhorn, 1999). In fact, autumn fattening may occur earlier than expected due to higher threshold photoperiod inducing changes in energy balance compared to captive animals, that were originally caught in southern Madagascar (Schmid & Kappeler, 1998; Génin & Perret, 2000).

Another hypothesis that may explain the lack of fattening is that March and April 1999 were exceptionally dry. Total rainfall reached 25 mm in Morondava compared with the average 130 mm (Sorg & Rohner, 1996; Institut National de Météorologie d'Antananarivo). Few fruits were available, and mouse lemurs fed mainly on gum and insects. *Microcebus murinus* has been shown to feed on gum occasionally (Martin, 1973). Nevertheless, in the drastic conditions of the early dry season, gums appeared as a keystone resource, as shown in other primate species inhabiting other environments (Bearder & Martin, 1980; Nash, 1986; Lindenmayer *et al.*, 1994; Power & Oftedal, 1996; Isbell, 1998; Heymann & Smith, 1999; Peres, 2000). Gums are found in patches and are rapidly renewed (Nash, 1986). *Terminalia* spp. were the most abundant gum trees. *Terminalia* gums have a high (87.8%) of soluble sugar and a low protein content (5.2%) (Hladik *et al.*, 1980). Thus, it may be possible for these gums to be assimilated by non-specialized species, but this would suggest a need for supplementary protein, which is likely to be provided by insects (Hladik *et al.*, 1980). The present study is the first to find evidence of interspecific competition between the Grey Mouse Lemur and the specialized gummivorous Fork-marked Lemur *Phaner furcifer* (Charles-Dominique & Petter, 1980).

At the beginning of the dry season, the spatial distribution of both sexes fitted the distribution of gum trees. However, several sex-specific differences indicate that males and females use different strategies. First, despite the overlap of home ranges, local spatial exclusion of males and females was observed, especially far from gum trees. Males entered fewer traps than females but were more often trapped where no female was trapped than the opposite. Second, female body mass was higher than male body mass, as has previously been shown (Hladik *et al.*, 1980; Schmid, 1999). Moreover, females trapped near gum trees were heavier than the others whereas the heaviest males were trapped near gum trees, and/or at capture locations where no female was trapped. Therefore, the higher body mass of females seems to be related to their dominance over males in feeding competition rather than physiological differences. In captivity, no significant difference in body mass appears between males and females fed *ad libitum* except when they are grouped (Génin & Perret, 2000; Génin, 2002). Competition for gum trees was confirmed by behavioural observations. In at least one case, an old and heavy female monopolized a gum tree, tolerating some animals and chasing others. Female dominance has been reported in the Grey Mouse Lemur as well as in several other prosimian primates (Young *et al.*, 1990; Tilden & Oftedal, 1995; Hemingway, 1999; Radespiel & Zimmermann, 2001).

During reproductive inactivity, the female spacing pattern seemed to be determined by the distribution of gum trees, whereas the spacing pattern of males was both determined by attraction to gum trees and avoidance of females. In contrast, attraction to females appears during the brief breeding season (~ 4 weeks) in accordance with the FIS hypothesis (Ostfeld, 1990; Eberle & Kappeler, 2002). At this period, the size of male home ranges has been shown to increase (Radespiel, 2000). Nevertheless, mouse lemur home ranges are known to be relatively stable (Eberle, pers. com.). Males with stable home ranges are likely to be dominant old males that are not closely related to females, as suggested in the Brown Mouse Lemur (Atsalis, 1999a). Like in this sibling species, one-year old males seem to be more erratic than old males with stable home-range (Atsalis, 1999b). Natal male dispersion has been observed in the Grey Mouse Lemur (Charles-Dominique, pers. com.) and in the closely related Brown Mouse Lemur (Atsalis, 1999b; Atsalis, 2000). Likewise, related females are found in large sleeping groups whereas males usually sleep alone (Radespiel *et al.*, 2000; Radespiel *et al.*, 2001). Female dominance in competition for gum trees in autumn agree with the model of local resource competition (LRC) and suggest an active mechanism for male dispersion (Clark, 1978). This model was developed on a lorimid nocturnal prosimian, *Otolemur = Galago crassicaudatus*, which is mainly gummivorous (Nash, 1986). Mouse lemurs are solitary foragers (Martin, 1973) and a succession of different individuals was observed on gum trees. An optimal size of matrilinear female group may enhance monopolization of gum trees. The model of local resource enhancement (LRE) predicts that female group size below this optimum leads to a female-biased natal sex ratio whereas natal sex ratio is male-biased when the female nucleus size is above the optimum (Schwarz, 1988). Indeed, captive females have been shown to overproduce daughters when they are housed individually whereas they overproduce sons when they are grouped or submitted to female urine odour (Perret, 1990, 1996; Perret & Colas, 1997).

The adult sex ratio may also be biased by differences in mortality and in use of space. Lower body mass and higher activity should lead to higher mortality in males. Predation has been shown to be extremely high in mouse lemurs, especially during the dry season (Goodman *et al.*, 1993). Only a few heavy males and the only very heavy male (101 g) were trapped near gum trees at female capture locations.

The heaviest male had been captured since 1996 and was thus at least 4 years old. Dominance in the context of mating competition has been shown to be highly correlated with age in captivity (Aujard & Perret, 1998). Such dominant males, which reach high body mass in the early dry season may have higher reproductive success than other males, as suggested in the Brown Mouse Lemur (Atsalis, 1999b). In the Kirindy forest, the sex ratio has been shown to fluctuate throughout the year (Schmid & Kappeler, 1998). During the dry season, fat reserves are used for prolonged torpor bouts that are mainly observed in females (Schmid, 1999). Most males remain active during the dry season and captures are highly male-biased in August and September (Schmid & Kappeler, 1998). Many new males are captured at this period and many of them are only captured once (Eberle, pers. com.). Based on the same observations on the Brown Mouse Lemurs, Atsalis (1999) has suggested that these males may correspond to young dispersing males. Captured males increase their body mass during this period (Schmid & Kappeler, 1998), taking advantage of the decrease of feeding competition during female hibernation. The drastic drop of body mass observed after the month of mating suggest that fat reserves are used for sexual competition in male mouse lemurs, rather than winter survival (Martin, 1972; Fietz, 1998; Atsalis, 1999b). In the same study area, Fietz (1998) found a positive correlation between male body mass and the distance to the nearest female in captures. In a different environment characterized by a reconstituted endemic forest surrounded by plantations, a female-biased “population nucleus” was described and contained a few “central males” of high body mass whereas most “peripheral males” of low body mass were found in the periphery fringe habitat (Martin, 1972). I propose that different spatial patterns observed may be explained by the distribution and the abundance of resources. In the Kirindy forest, gum trees appeared as a keystone resource patchily distributed. Sex ratio was female-biased (58%) indicating that the study area corresponds to the “population nucleus”. Extra captures out of the study area showed that we did not trap the population entirely and the presence of “peripheral males” out of the study area cannot be excluded (Génin & Eberle, unpublished data).

Although some dominant males with stable home-range might occur, female Grey Mouse Lemurs were generally dominant over males in feeding competition for keystone resource gum trees. Consequently, they reached higher body mass at the end of the period of seasonal fattening. Moreover, local monopolization of food by matrilineal female groups may provide a possible mechanism for male natal dispersion and female bonding in a context of patchily dispersed resources. This study suggests that the differences noted in socio-spatial organization of the Grey Mouse Lemur are due to differences in spatial dispersion of food during the critical period of dry season.

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