



Social System of *Microcebus berthae*, the World's Smallest Primate

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*Our goal was to provide a first characterization of the social system of pygmy mouse lemurs (*Microcebus berthae*), the world's smallest primate species. During a 4-mo field study of 12 females and 27 males, we combined capture-recapture and morphometric data with detailed behavioral observations of individually marked subjects and genetic paternity analyses of a population in Kirindy Forest, western Madagascar. We describe the social organization of *Microcebus berthae* as a solitary forager living in an individualized neighborhood system characterized by extensive intra- and intersexual home range overlap of adult individuals within a male-biased population. Male and female pygmy mouse lemurs inhabited home ranges (males: 4.9 ha; females: 2.5 ha) that are more than twice as large as those of sympatric *Microcebus murinus*. On average, pygmy mouse lemurs of both sexes spent about half of the days sleeping alone. Preliminary analysis of genetic population structure suggests female philopatry and male dispersal. Sleeping associations of variable composition that consisted not preferentially of close relatives and proximity during part of the nightly activity contributed together with regular social interactions to the maintenance of a social network. The spatial distribution pattern of adult males and females, the absence of sexual size dimorphism, relatively large male testicular volume and moderate female estrous synchrony suggest a promiscuous mating system with a high potential for scramble competition. In general, there are many similarities between the*

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social system of Microcebus berthae and those of other Microcebus spp. However, striking differences with sympatric gray mouse lemurs (Microcebus murinus) in female home range size, dispersion and sleeping behavior indicate the existence of species-specific socioecological adaptations in closely related species occupying very similar ecological niches.

KEY WORDS: social system; solitary primate; *Microcebus berthae*; sleeping associations; mating system; social structure; Kirindy.

INTRODUCTION

Understanding the evolution of primate social systems is a major goal in primatology (Crook and Gartlan, 1966; Eisenberg *et al.*, 1972; Clutton-Brock, 1974; Smuts *et al.*, 1987; Müller and Thalmann, 2000; Kappeler and van Schaik, 2002). Cheirogaleids, together with the galagids and lorises, may resemble the ancient primates most closely (Charles-Dominique and Martin, 1970; Martin, 1972; Charles-Dominique, 1974; Eisenberg, 1981), providing a baseline from which to model primate social evolution (Kappeler *et al.*, 2002). With 8 currently described species, mouse lemurs (*Microcebus spp.*) are the most diverse taxon among the cheirogaleids (Rasoloarison *et al.*, 2000; Yoder *et al.*, 2000). Their small body size, high population densities and wide geographic distribution across Madagascar offer the opportunity to study adaptations and their consequences to a large range of life-history strategies and diverse habitats ranging from evergreen rain forests to dry deciduous and spiny forests (Kappeler, 2000b).

Our current knowledge about mouse lemur social systems primarily comes from several long-term field studies of gray mouse lemurs, *Microcebus murinus* (Martin, 1972, 1973; Fietz, 1998, 1999a; Schmid and Kappeler, 1998; Radespiel, 2000b; Radespiel *et al.*, 2001a, 2001b; Eberle and Kappeler, 2002, 2004a, 2004b). Despite wide distribution throughout southern and western Madagascar, reports of their social organization have been remarkably uniform. Males and females are spatially dispersed and forage solitarily in extensively overlapping home ranges within a population that is organized in clusters of closely related females (matrilines) (Wimmer *et al.*, 2002). The social structure of *Microcebus murinus* is characterized by a network of individualized social relationships maintained through acoustic and olfactory communication, stable sleeping associations of related females and occasional social interactions (Charles-Dominique, 1978; Pagès-Feuillade, 1988; Radespiel, 2000a; Radespiel *et al.*, 1998, 2001a; Wimmer *et al.*, 2002). Because of extensive home-range overlap, both sexes have potential access to more than one mating partner. The mating system of

gray mouse lemurs was therefore inferred to be a promiscuous one in which males compete over access to fertile females via contest and scramble competition (Schmelting, 2000; Radespiel *et al.*, 2001a). Recent direct observations of mating interactions, in combination with genetic parentage analyses, confirmed the existence of a highly promiscuous mating system (Eberle and Kappeler, 2004a, 2004b).

Much less is known about the social systems of other mouse lemurs. Mark-recapture data suggested a high degree of inter- and intrasexual spatial overlap in brown mouse lemurs, *Microcebus rufus* (Harcourt, 1987; Atsalis, 2000), but detailed behavioral studies of individuals have not been conducted. A preliminary study of golden brown mouse lemurs, *Microcebus ravelobensis*, revealed broad similarities in the mating system and social organization to gray mouse lemurs (Weidt *et al.*, 2004). The social systems of *Microcebus griseorufus*, *M. myoxinus*, *M. tavaratra* and *M. sambiranensis* are unstudied in the field.

The 30-g pygmy mouse lemurs (*Microcebus berthae*) are the smallest extant primate. First discovered in 1992 in the dry deciduous forest in western Madagascar (Schmid and Kappeler, 1994) they were initially thought to represent a rediscovery of *Microcebus myoxinus* (Peters, 1858), but comparative morphometric and genetic studies revealed their status as a new species (Rasoloarison *et al.*, 2000; Yoder *et al.*, 2000). They appear to be restricted to the Kirindy Forest and the nearby Réserve Spécial d'Andranomena in the Menabe Region of western Madagascar, where they are sympatric with 60-g gray mouse lemurs (*Microcebus murinus*) and 3 other cheirogaleids: *Cheirogaleus medius*, *Mirza coquereli* and *Phaner furcifer* (Ganzhorn and Kappeler, 1996; Schwab and Ganzhorn, 2004). Whereas basic aspects of the social systems of these sympatric cheirogaleids have been described recently at Kirindy (Kappeler, 1997b; Fietz, 1998, 1999a, 1999b; Kappeler *et al.*, 2000; Fietz *et al.*, 2000; Eberle and Kappeler, 2002, 2004a, 2004b; Schülke and Kappeler, 2003; Schülke, 2003; Schülke *et al.*, 2004), *Microcebus berthae* has only been the object of an ecophysiological (Ortmann *et al.*, 1996, 1997; Schmid, 1996; Schmid *et al.*, 2000) and a mark-recapture study (Schwab, 2000; Schwab and Ganzhorn, 2004). The latter study indicated that pygmy mouse lemurs have a promiscuous mating system and seem to be less social than other solitary prosimians are, but the conclusions are based on indirect evidence.

The aim of our study was to characterize the social system of pygmy mouse lemurs in more detail, using the recently suggested differentiation of social systems into social organization, social structure and mating system by Kappeler and van Schaik (2002) as a framework. We used a combination of morphometric data, behavioral observations and genetic analyses via

microsatellites to characterize a population of the world's smallest primate in Kirindy Forest.

METHODS

Study Site

We studied pygmy mouse lemurs in the Forêt de Kirindy/CFPF, a dry deciduous forest in western Madagascar, *ca.* 60 km northeast of Morondava (44°39'E, 20°03'S, 30–60 m above sea level). The study site is located within a 12500-ha concession of the Centre de Formation Professionnelle Forestière (CFPF) de Morondava. The climate is characterized by pronounced seasonality with a hot rainy season between December and March and little or no rainfall from April to November (Ganzhorn, 1995; Sorg and Rohner, 1996; Schmid and Kappeler, 1998). The forest is very dense with a comparatively low canopy; most trees do not exceed 20 m in height (for additional information see Sorg *et al.*, 2003).

We defined the study area within the concession (locally known as N5) by the boundaries of a grid system of small foot trails. Within a 500 × 500-m core area, there is a rectangular system of small trails at 25-m intervals, surrounded by additional trails at 50- and 100-m intervals. Each trail intersection is marked for orientation, and their coordinates were used to create a map (Zinner *et al.*, 2003).

Capture and Marking

We baited Sherman live traps with pieces of banana and set them near trail intersections 0.5–2 m above ground for 3 consecutive nights in one-half of the study area (12.5 ha) and then 3 consecutive nights in the other half of the study area (12.5 ha) in early August, early(A) and late(B) September, late October, mid-November 2002, and during 4 nights in late November at the end of the study period. We opened and baited traps at dusk and checked and closed them at dawn. To minimize interference with nocturnal mating activities, we checked all traps additionally in the first half of the night in November so that no lemur was detained for more than a few hours. We used a total of 210–231 traps per night. We collected subjects in the early morning and kept them at a nearby research station during the day.

We briefly restrained and immobilized newly captured pygmy mouse lemurs with 10 μ l Ketanest 100 (Rensing, 1999) and marked them individually with subdermally implanted microtransponders (Trovan, Usling, Germany). To facilitate individual recognition at night, we also marked subjects by shaving unique patterns on their tails. We took tissue samples in

form of small (2–3 mm²) ear biopsies on both sides for later DNA extraction and genetic analysis from all captives. We weighed every new captive, examined it for injuries and reproductive state (after Buesching *et al.*, 1998) and took a set of standard morphometric measurements, including canine height and testes length and width (Schmid and Kappeler, 1994; Kappeler, 1997a). We calculated testicular volume from testicular length (TL_{left} and TL_{right}) and width (TW_{left} and TW_{right}) as the volume of 2 spherical ellipsoids: $V = (\pi \times \text{TL}_{\text{left}} \times \text{TW}_{\text{left}}^2)/6 + (\pi \times \text{TL}_{\text{right}} \times \text{TW}_{\text{right}}^2)/6$. We only identified recaptured individuals from the same trapping session. We identified, weighed and measured testicular size for recaptured animals from previous trapping sessions. We released all captives at the site of capture shortly before dusk.

Focal Observation

For direct focal observation (Altmann, 1974) a total of 28 (9 f/19 m) subjects were equipped with 2-g radio collars (TW4, Biotrack, UK) that lasted between 7 and 50 days. We followed focal subjects during their nocturnal activity for 1–2 h before switching to another subject. We recorded the location of a focal animal every min and recorded behavioral data cumulatively for observation intervals of 1 min (one-zero sampling). Whenever conspecifics were nearby, we recorded their distance and identity. We defined as social encounters all approaches to ≤ 5 m of the focal animal. A re-entry into the 5m-radius after ≥ 5 min was a new encounter. The observation time is opportunistic, but it was spread evenly over one statistical night (18:00–6:00h) for every subject. In total, we observed pygmy mouse lemurs for 188 h. Because of their small size and the dense vegetation, females could only be located in 62.5% (range 61.6–70.2%) and males in 57.9% (range 52.7–79%) of the 1-min samples. Behavioral observations during complete minute intervals were possible for females in 44.8% (range 40.3–51.7%) and for males in 28.8% (range 21.5–49.6%) of the observation time. The difference between the sexes is due to males moving faster and longer distances.

Home Range Analyses

We transformed spatial information from capture sites, sleeping sites, direct observation and additional radio-tracking into x- and y-coordinates. We calculated 100% minimum convex polygons (MCP) and home range overlap via Animal Movement Software (Hooge *et al.*, 1999) and an unpublished script (O. Unger and F. Torkler, 2000) for ArcView GIS 3.2 (Esri).

Individual female home range size estimates ($n = 4$) are based on 13 (range 12–14) h of focal observation and an additional 33 (range 22–37) independent locations such as sleeping sites, trap sites and additional observations. Individual male home range size estimates ($n = 5$) are based on 19 (range 11–25) h of focal observation and an additional 35 (range 27–50) independent locations.

Nightly Path Length and Home Range Use

The short time interval (1 min) between subsequent locations of the focal lemur and the detailed spatial data within the narrow grid-system made it possible to estimate minimum nightly path length. We calculated the path length of every observation hour as the sum of all distances between subsequent locations of the subject. To calculate the path length of one statistical night per lemur we added the average path lengths of every hour between 18:00 h and 6:00 h. To assess intensity of home range use, we calculated a usage index UI as the relation of nightly path length (L) to perimeter (d) of the home range: $UI = L/d$. We calculated the perimeter as the perimeter of a circle with the same area (A) as the corresponding home range of the lemur: $d = 2 \times \sqrt{(A/\pi)}$.

Sleeping Associations

During daytime, we determined sleeping sites of radiocollared subjects by triangulation and visual inspection. We marked every sleeping site with flagging tape. We determined the composition of sleeping associations of radiocollared individuals via direct observations at the onset of activity, using individual shaving patterns and external genitalia as cues. Based on average observed frequency of solitary sleeping, we calculated expected values for individual males and females.

Genetic Analyses

We obtained tissue samples for genetic analyses from 38 animals trapped between August and November 2002. We immediately transferred them to 70% ethanol and stored them for ≤ 6 mo. We isolated DNA per standard protocols (Qiagen QIAmp DNA Mini Kit No. 51306). For microsatellite analysis, we used 10 nuclear loci, which had been developed for *Microcebus murinus* or *Cheirogaleus medius* (33.103) (Hapke *et al.*, 2003, except Mm35 which had been developed for *M. murinus* by the authors but

was not used to test for polymorphism). We performed wax mediated hot-start PCRs in 30 μ l reaction volume containing 0.5 U/ μ l AmpliTaq (Perkin Elmer), 10 pmol of each primer, 3.75 pmol of each dNTP, 10 mM Tris-HCl (pH 8.4), 50 mM KCl, 2 mM MgCl₂, 0.1% Triton X-100, 1.2 mg/ml BSA and about 10 ng of template DNA in a Thermocycler PTC-200 (MJ-Research) (Hapke *et al.*, 2003). An initial denaturation step of 2 min at 92°C was followed by 38 (Mm22, Mm30, Mm39, Mm40, Mm42, Mm43b, 33.103) or 40 (Mm21, Mm35) cycles of 40-sec denaturation at 92°C, 1-min annealing at 58°C or 54°C (only Mm30), 1-min elongation at 72°C and a final extension for 5 min at 72°C. The primers were fluoro-labelled and PCR products were separated and visualized on standard 4.5% acrylamid gels (Accugel, National Diagnostics) on LiCOR DNA-Sequencer (long readir 4000 or 4200). We determined size of alleles visually using length standards. We calculated allelic frequencies, observed and expected heterozygosity, and tests on deviation from Hardy-Weinberg-Equilibrium via Cervus 2.0 software (Marshall *et al.*, 1998).

We performed parentage analyses on the basis of combined mismatches and likelihood analysis via Cervus 2.0 software (Marshall *et al.*, 1998). We excluded candidate parents if ≥ 2 homozygous or 1 heterozygous mismatch occurred. The likelihood analysis for nonexcluded candidates is based on detailed parentage simulation (10000 runs, 100 candidate parents, assumption of: 0.7 sampling rate, 0.89 average loci typing rate, 0.01 error rate) to estimate the resolving power of the used loci and to estimate critical values to evaluate the parentage analysis statistically. Additionally, we estimated relatedness among individuals via the parameter R calculated from the allelic frequencies at the 10 microsatellite loci with Relatedness 5.08 (Queller and Goodnight, 1989).

Statistical Analyses

We performed all statistical tests via Statistica 6.0 (StatSoft). Due to small sample size, we mostly used nonparametric tests. All tests are 2-tailed with alpha at 0.05.

RESULTS

Population Ecology

In 7719 trap nights between August and November 2002, we caught a total of 39 adult *Microcebus berthae* 140 times. Most individuals were caught more than once (≤ 11 times). There was no general sex difference

in trapability as shown by the frequency distributions of recaptures (Kolmogorov-Smirnov-Test, $D = -0.03$, ns). Overall, the proportion of recaptured individuals increased from the third trapping sessions onwards (Sep-B: 2/11; Oct: 7/10; Nov: 25/33), indicating that we knew most of the population at the end of the study. Throughout the entire study period the sex ratio was male-biased (27 males vs. 12 females) (χ^2 -Test, $\chi^2 = 5.77$, $df = 1$, $p < 0.05$).

Morphometrics

We obtained morphometric data from 26 adult males and 11 adult females. There was no sexual dimorphism in skull length, tail length or canine height (Table I). However, females were on average larger than males in head-body length and head width. Overall, body mass of adult males (median: 33 g, $n = 27$) did not differ from adult females (median: 33 g, $n = 11$). However, males and females showed different dynamics in body mass over the study period. Outside the mating season females were heavier than males (median: females 32 g (range 32–37) vs. males 31 g (range 29–35), Mann-Whitney U, $z = 2.21$, $p < 0.05$; $n = 5$ females and 12 males). With the approaching mating season males increased in body mass by 10%, eliminating the previous sex difference in body mass (median: females 33 g (range 31–37) vs. males 34 g (range 28–39), Mann-Whitney U, $z = -0.51$, ns, $n = 6$ females and 15 males).

Reproductive Condition of the Sexes

Male testicular volume varied seasonally, increasing 5-fold until the end of October (Fig. 1). In males caught for the first time, testicular volume is positively correlated with capture date until a peak in October (Spearman

Table I. Measurements of adult male and female *Microcebus berthae* caught between August and November 2002

Variable (mm)	Males (n = 26)			Females (n = 11)			z	p
	Median	Min	Max	Median	Min	Max		
Head-body length	118.5	106.0	131.0	127.0	123.0	136.0	3.24	0.001
Head length	30.8	29.5	32.1	31.0	29.6	31.9	0.23	ns
Head width	19.1	18.3	20.5	19.5	19.0	19.8	2.64	0.008
Tail length	126.5	115.0	138.0	125.0	118.0	134.0	-0.22	ns
Canine length	1.7	1.1	2.2	1.7	1.2	1.9	-0.07	ns

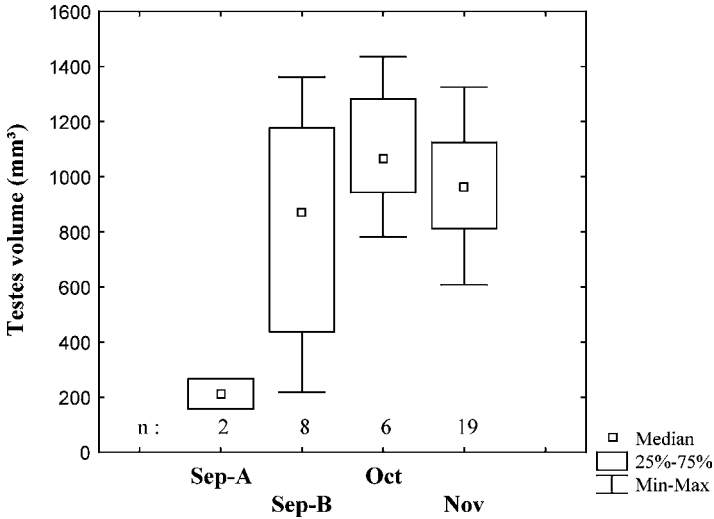
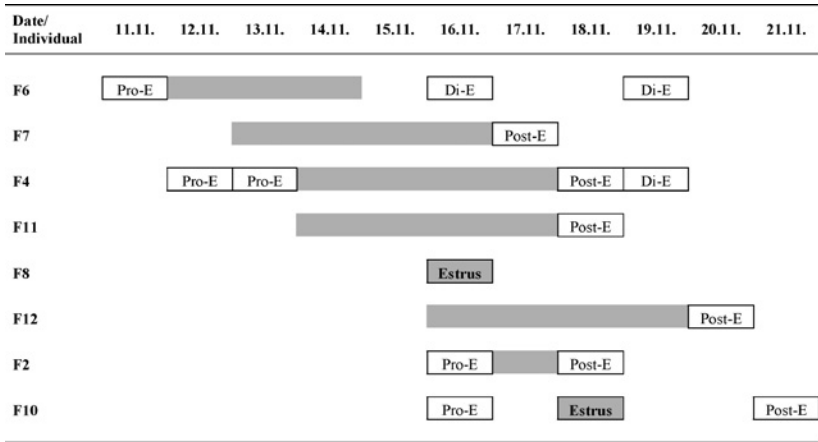


Fig. 1. Seasonal change in testicular volume in male *Microcebus berthae*. For September, values from the first (Sep-A) and second (Sep-B) half of the month are shown.

rank correlation, $r = 0.59$, $n = 17$, $p < 0.05$). Using the regression between testicular volume and body mass based on a data set of 24 wild populations of Malagasy primates by Schülke *et al.* (2004) (\log testicular volume = $2.03 + 0.38 \times \log$ body size) the value for *Microcebus berthae* is above the expected value. Female vulval morphology changed only in November. We caught the first pro-estrous females on November 11. All 8 females captured in the 10 days thereafter showed signs of reproductive activity: 2 had an open vagina and 3 others were captured shortly before and after estrus, respectively. The reconstruction of the temporal distribution of their likely estrous days is shown in Fig. 2 and reveals that on most nights only one female was likely to be in estrus.

Home Range and Nightly Path Length

Male *Microcebus berthae* used on average larger home ranges than females (Mann-Whitney U, $z = -2.45$, $p < 0.05$; males: 4,92 ha; females: 2,50 ha) (Fig. 3). A preliminary analysis showed that home range size reached an asymptote after a cumulative observation time of 12 h for females and 15 h for males. There is no correlation between home range size



Estrus – vagina open, and perigenital skin swollen; Pro-E: Pro-Estrus – perigenital skin swollen and partly reddened; Post-E: Post-Estrus: vagina closed and perigenital skin re-sealed; Di-E: Di-Estrus: vagina and perigenital skin not swollen

Fig. 2. Temporal distribution of female estrus during the mating season mid-November, gray marked are individual time windows of known or potential estrus.

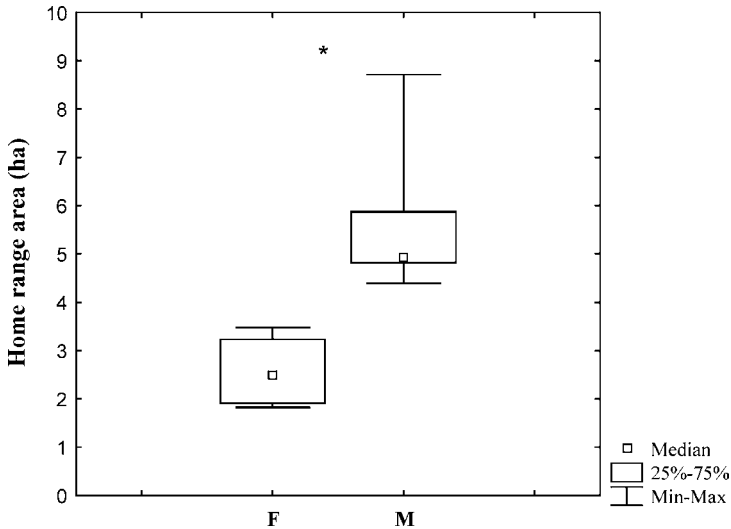


Fig. 3. Median size of MCP home range areas of female (n = 4) and male (n = 5) *Microcebus berthae*. Males inhabited larger ranges than females (Mann-Whitney U, z = -2.45, p < 0.05).

and the number of data points used for the analysis (Spearman rank correlation, $r = 0.41$, $n = 9$, ns). Female home ranges were not exclusive and overlapped with those of 1 or 2 other females on average by 24%. Males shared their home ranges with ≤ 9 other males (median: 7). Males ($n = 4$) traveled on average 4470 m per night, females ($n = 4$) 3190 m. Males and females used their home ranges extensively. Their minimum nightly path length varied between 11 and 22 times the perimeter of the home range (UI).

Sleeping Associations

Generally, males and females slept with others about every second day (females: 28 of 58, males: 59 of 129). However, individual variation was very high (Fig. 4). Some males and females slept more often alone, others more frequently together with conspecifics than expected by chance. Female-female (on $n = 7$ control days), male-male (on $n = 14$) and mixed-sex sleeping associations (on $n = 14$) (female with ≤ 4 males) occurred. Some sleeping groups were stable in composition over several days and used ≤ 4 different sleeping sites together. Based on spatial overlap data, 283 dyads could have potentially shared a sleeping site; however, only 15 of them were actually found in sleeping associations.

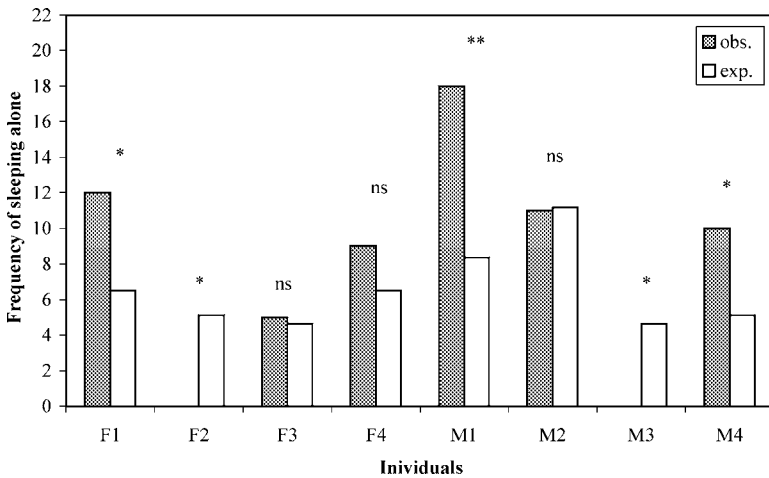


Fig. 4. Observed and expected frequencies of solitary sleeping in 4 female and 4 male *Microcebus berthae* (Chi²-Tests, *indicates $p < 0.05$ and ** $p < 0.001$). Expected values are based on average frequency of sleeping solitarily.

Proximity, Social Encounters and Social Behavior

Females and males spent 15% of observation intervals in proximity (≤ 10 m) of conspecifics. In 11% (females) or 9% (males) of observation intervals there was close proximity (< 1 m). In 188 observation h, 56 social encounters between 2 or 3 individuals occurred. Eleven encounters occurred at the nest site and 45 occurred during the nightly activity. Mixed-sex encounters ($n = 16$) were most frequent; interactions between 2 or 3 males ($n = 13$) were also very common. Females interacted less frequently with same-sex conspecifics ($n = 3$). In general, males ($n = 4$; 0.93 interactions/hour) interacted more frequently with conspecifics than females did ($n = 4$; 0.49 interactions/hour), and they had more social encounters with females and fewer with males than expected (Chi²-Test, $\chi^2 = 4.67$, $df = 1$, $p < 0.05$; male-female: observed 16 vs. 8 expected; male-male: observed 12 vs. 20 expected). Thirteen of the 23 social encounters for which the identity of the partners was known occurred between sleeping partners; many of them at the nest site ($n = 6$).

In both sexes social behavior occurred only in a small proportion (7–8% of observation intervals, $n = 1511$) of the activity. Agonistic behaviors, such as chasing or grabbing with biting occurred in 6 of the 40 interactions in different contexts: feeding ($n = 3$), sexual ($n = 1$) and others ($n = 2$). Affiliative interactions lasted only a few minutes and were characterized by mutual grooming and huddling. However, huddling bouts of up to 23 min occurred occasionally. In general, interactions between males did not differ qualitatively from female-female interactions.

Genetics

The genetic variability of the microsatellites is high and ranged between 4 and 12 alleles and observed heterozygosities from 0.42 to 0.92 (Table II). Only Mm53 has low heterozygosity of 0.18. Overall observed heterozygosity is 0.67. Due to small allelic number, deviation from Hardy-Weinberg-Equilibrium could not be tested for all loci.

The average relatedness among individuals of the population was low for both adult females dyads ($r = 0.0485$, $n = 55$) and adult males dyads ($r = -0.0069$, $n = 351$). Adult females were on average more closely related than adult males (Mann-Whitney U, $z = 1.96$, $p < 0.05$). However, males and females did not differ in the number of closely related individuals ($r \geq 0.2$) within the population (Mann-Whitney U, $z = -0.16$, ns). Females had on average 5 (range 0–7, $n = 11$) and males 4 (range 0–11, $n = 27$) close relatives. However, 37% of males, but only 18% of females had > 5

Table II. Characterization of 10 microsatellite loci. Number of alleles, number of adult *Microcebus berthae* individuals typed (n), expected (exp) and observed (obs) heterozygosity (H) are shown

Locus	Allele	n	H (obs)	H (exp)
33.103	12	37	0.84	0.86
Mm21	4	35	0.51	0.47
Mm22	9	38	0.90	0.84
Mm30	6	38	0.76	0.60
Mm35	12	38	0.92	0.88
Mm39	10	38	0.90	0.83
Mm40	7	38	0.82	0.83
Mm42	11	26	0.50	0.87
Mm43b	5	38	0.42	0.68
Mm53	4	11	0.18	0.26

close relatives. Two males with central home ranges had no close relative within the population, but only 1 female with a peripheral home range lived without relatives in her vicinity.

The average relatedness of female dyads that overlapped spatially or were close neighbors ($r = 0.0747$, $n = 24$) did not differ from spatially separated female dyads ($r = 0.0282$, $n = 31$) (Mann-Whitney U, $z = 1.37$, ns). Similarly, there was no difference in the number of close relatives (4 vs. 5) (Chi²-Test, $\chi^2 = 0.0$, $df = 1$, ns) or potential mother-daughter/sister-pairs (2 vs. 4) between neighboring and more distantly located females (Chi²-Test, $\chi^2 = 0.29$, $df = 1$, ns). Spatially overlapping male dyads ($r = 0.0038$, $n = 80$) did not differ from spatially separated male dyads ($r = -0.0100$, $n = 271$) in their average relatedness (Mann-Whitney U, $z = -0.79$, ns). However, the proportion of dyads consisting of close relatives was smaller in males with overlapping home ranges (5 of 80) than in spatially separated males (44 of 271) (Chi²-Test, $\chi^2 = 5.13$, $df = 1$, $p < 0.05$). The proportions of potential father-sun/brother dyads did not differ (Chi²-Test, $\chi^2 = 0.72$, $df = 1$, ns).

The average relatedness of cosleeping dyads ($r = 0.0153$, $n = 15$) did not differ from dyads that overlapped spatially, but did not sleep together ($r = -0.0303$, $n = 268$) (Mann-Whitney U, $z = -0.90$, ns). Also, the proportion of close relatives did not differ between actual (3 of 15) and potential cosleeping dyads (24 of 268) ($\chi^2 = 2.01$, $df = 1$, ns). Close kin among sleeping associations were 2 male-male dyads and one male-female dyad, which was a potential parent-offspring or sister-brother pair.

DISCUSSION

The main results of our study indicate that pygmy mouse lemurs are solitary foragers that live in an individualized neighborhood system. Their

social organization is characterized by extensive intra- and intersexual home range overlap of adults within a male-biased population. The genetic population structure revealed a potential for female philopatry and male dispersal. Sleeping associations of variable composition, which consisted not preferentially of close relatives, and proximity during part of the nightly activity and regular social encounters contributed to the maintenance of a social network. A promiscuous mating system with a high potential for scramble competition is suggested by the spatial distribution pattern, the absence of sexual dimorphism, high male testicular volume and moderate female estrous synchronization. Below, we discuss these points in more detail.

Social Organization

Sex Ratio

The sex ratio of the Kirindy pygmy mouse lemur population was uneven with *ca.* 2 males per female over the entire study period, which was not an effect of a general sex difference in trapability. A sex difference in seasonal activity patterns like that of *Microcebus murinus* (Fietz, 1998; Schmid and Kappeler, 1998) and possibly *M. rufus* (Atsalis, 1999), where females undergo prolonged periods of inactivity in the cold dry season, is unlikely for pygmy mouse lemurs. First, the sex ratio was unbalanced in every study month, also at the beginning of the rainy season. Second, *Microcebus berthae* females do not hibernate (Ortmann *et al.*, 1996, 1997; Schmid, 1996; Schmid *et al.*, 2000).

Male-biased sex ratios are unusual for primates in general (Clutton-Brock and Iason, 1986; Dunbar, 1987; van Schaik and de Visser, 1990), but not for lemurs (Kappeler, 2000a): *Cheirogaleus medius* (Müller, 1999; Fietz, 1999b), *Microcebus rufus* (Harcourt, 1987; Atsalis, 2000), *M. murinus* (Fietz, 1998; Schmid and Kappeler, 1998; Radespiel, 1998, 2000b) and *Phaner furcifer* (Schülke *et al.*, 2001). Possible mechanisms for unbalanced adult sex ratios are sex-biased juvenile or adult mortality (Clutton-Brock *et al.*, 1977) and manipulation of the birth sex ratio (Perret, 1990, 1996; van Schaik and Hrdy, 1991). Neither captivity (Perret, 1990) nor field data (M. Eberle, pers. comm.) suggest sex-biased mortality in gray mouse lemurs. Similarly, female-biased mortality is unlikely in the Kirindy population, because the only recaptures of formerly marked lemurs (during a pilot study 2–3 yr ago) were females. In general, one would predict higher mortality in the dispersing sex, i.e., males in most primates (Cheney and Wrangham, 1987). Captive gray mouse lemurs bias birth sex ratios in favor of one sex in certain social circumstances (Perret, 1996; Colas, 1999).

However, in the field, Martin (1972) observed even sex ratios of young in the nest.

Martin (1972, 1973) suggested that (gray) mouse lemur populations are structured in discrete nuclei in which females and a few dominant males form the center, and the majority of males are forced to live in the periphery. This population nucleus would result in strong local differences in the sex ratio: female-biased in the center and male-biased in the periphery. However, we found no evidence that the Kirindy pygmy mouse lemur population was situated at the periphery of a population nucleus because we trapped a considerable number of females and their home ranges covered nearly the entire study area.

The observed male-biased sex ratio, in combination with the short and not tightly synchronized estrus of females, should result in a strong male-biased operational sex ratio, as in *Microcebus murinus* (Eberle and Kappeler, 2002), and, thus, in intense intrasexual competition among males. However, the mechanisms and the adaptive value of male-biased sex ratios in pygmy mouse lemurs and other lemurs (Kappeler, 2000a) remains unknown (for a general review see Cockburn *et al.*, 2002).

Sleeping Associations

In contrast to Schwab (2000), we observed regular sleeping associations in pygmy mouse lemurs, preferentially in large leaf nests built by a sympatric cheirogaleid, *Mirza coquereli* (Sarikaya and Kappeler, 1997). On average, males and females spent every second day together with conspecifics at the same sleeping site. However, individual variation was high and some males and females preferred to rest solitarily. Mixed-sex sleeping associations were common; several females regularly associated with ≤ 4 males. In addition to female-female associations, there were all male sleeping groups, which contrasts with *Microcebus murinus*, in which predominantly close female relatives form long-term sleeping groups and males sleep alone most of the time (Martin, 1972; Pagès-Feuillade, 1988; Radespiel, 1998, 2000b; Radespiel *et al.*, 1998, 2001b; Wimmer *et al.*, 2002). In golden brown mouse lemurs, mixed-sex sleeping associations also occur frequently, but males sleep only rarely together (Weidt *et al.*, 2004).

Several hypotheses might explain sleeping group formation in solitary foragers. First, additional individuals at the sleeping site could provide energy savings via thermoregulatory advantages (Vickery and Millar, 1984; Schmid, 1997; Kappeler, 1998; Radespiel *et al.*, 1998; Aujard *et al.*, 2002). Huddling could protect against cooling in the morning and might also delay heating of torpid animals during the day (Schmid, 1997). In that case, mouse lemurs should form sleeping groups preferentially when temperature

fluctuations are highest and food shortage is most severe. However, in *Microcebus berthae* there is no seasonal fluctuation in the tendency to form sleeping associations during the transitional period between dry and wet season spanned by our study. In addition, they preferred relatively open sleeping sites, e.g., leaf nests, between leaves and lianas etc., though holes in living trees seem to have the best insulation capacities (Schmid, 1998). Thermoregulatory characteristics of leaf nests have not been described.

Second, cosleeping could reduce predation risk due to higher chance of predator detection or dilution effects or both (Kappeler, 1998; Bednekoff and Lima, 1998). Mouse lemurs face intense predation pressure by carnivores, raptors and snakes; predator attacks at sleeping sites were observed by Goodman *et al.* (1993) and Rasoliarison *et al.* (1995). Again, the preference for unsheltered sleeping sites by *Microcebus berthae* remains to be explained. However, our observations showed that they prefer protected sites, such as leaf nests and hole-like structures. Conversely, additional individuals also reduce crypsis and could increase predation risk at sleeping sites. Clearly, we need to understand in detail which strategies predators use (Bednekoff and Lima, 1998) and how sociality affects an individual's likelihood of predation (Janson and Goldsmith, 1995).

Third, high-quality sleeping sites could be limited in the forest, leading indirectly to the formation of sleeping groups (Schmid, 1997; Radespiel *et al.*, 1998). Optimal tree holes could indeed be limited for *Microcebus murinus* in some forests (Radespiel *et al.*, 1998) but not in others (Schmid, 1997). Because *Microcebus berthae* uses a wide variety of different sleeping sites, often without any special structure, a limitation of sites in the highly structured Kirindy dry forest seems unlikely.

It could be argued that advantages of cosleeping should preferentially be shared with close kin (Hamilton, 1964), leading to sleeping associations of closely related females in populations with female philopatry, as in *Microcebus murinus* (Radespiel *et al.*, 2001b; Wimmer *et al.*, 2002) and possibly other solitary primates (*Galago zanzibaricus*: Harcourt and Nash, 1986; *Galagoides demidoff* and *G. allenii*: Charles-Dominique, 1977). Nevertheless, also in mixed-sex sleeping associations, advantages could preferentially be shared with close relatives. The genetic composition of sleeping associations may suggest ultimate factors that lead to their formation. Three general possibilities exist: 1. sleeping groups consist of females with male and female offspring of the last season(s); 2. family groups, as in *Cheirogaleus medius* (Müller, 1998, 1999; Fietz, 1999b), composed of an adult pair and their offspring sleep together; and 3. unrelated individuals share the advantages of cosleeping opportunistically. Our preliminary analysis of *Microcebus berthae* genetic structure indicate that only 20% of sleeping group members were close relatives, a proportion that is similar,

to spatially overlapping but non-cosleeping dyads. Only one male-female dyad of cosleeping group members was a potential parent-offspring/sister-brother dyad. Additionally, the average relationship of actual sleeping group dyads was not different from those of potential cosleeping dyads, which never shared a sleeping site. We therefore conclude that sleeping associations have a more opportunistic character in pygmy mouse lemurs, in the sense that advantages are shared among individually known conspecifics and not exclusively among close kin. Because mouse lemurs have one of the highest mortality rates among primates, the pattern might be due to the scarcity of close relatives in the neighborhood, which decreases the opportunity for kin selection. Which fundamental advantage leads to sleeping group formation in *Microcebus berthae* and which mechanisms individuals use to find each other remains obscure.

Spatial Patterns

Kirindy female pygmy mouse lemurs used much larger home ranges (2.5 ha) than reported in a preliminary study based on capture-recapture data alone (1.2 ha: Schwab, 2000). Moreover, their home ranges are considerably larger than those of other mouse lemur species (*Microcebus murinus*: 0.7–1.8 ha (Pagès-Feuillade, 1988; Radespiel, 2000b; Eberle and Kappeler, 2002, 2004b); *M. ravelobensis*: 0.5–0.6 ha (Weidt *et al.*, 2004)), and about the same size as those of sympatric female *Mirza coquereli* (3 ha), which are 10-times larger than *M. berthae* (Kappeler, 1997b).

Because female home range size is mainly determined by the occurrence and distribution of resources, they reflect the average daily metabolic need (Emlen and Oring, 1977; Harvey and Clutton-Brock, 1981). In strongly seasonal ecosystems, such as the dry deciduous forests of western Madagascar, the time of lowest resource availability should determine minimum home range size. In fact, it could be shown that in areas with low resource supply, populations of a species use larger home ranges, versus populations in high-quality areas (Clutton-Brock, 1972; Tew and Macdonald, 1994; Lurz *et al.*, 2000). Species-specific physiological strategies to survive times with low resource availability could also lead to differences in home range size. During the cool dry season when food is in short supply, female gray mouse lemurs enter a seasonal torporous state (hibernation) (Petter-Rousseaux, 1980; Schmid, 1996, 1997; Schmid and Kappeler, 1998). *Microcebus berthae* only entered spontaneous daily torpor and did not hibernate (Ortmann *et al.*, 1996, 1997; Schmid, 1996; Schmid *et al.*, 2000). Pygmy mouse lemurs might instead compensate food shortages with enlarged home ranges, a strategy also used by spectral tarsiers (*Tarsius spectrum*: Gursky, 2000a) and squirrel monkeys (*Saimiri oerstedii*: Boinski, 1987).

Social Interactions and Proximity

As is typical for a solitary forager, temporal and spatial cohesion during nocturnal activity was low between individual *Microcebus berthae*, both in cosleepers and non-cosleepers. Apart from sleeping associations, conspecifics were in close proximity for on average 15% (ca. 2 h) of nightly activity, which corresponds to observations in other solitary foraging primates, e.g. *Microcebus murinus* (Pagès-Feuillade, 1988) and *Tarsius spectrum*, which spend ca. 11% of night activity in physical contact and additionally 17% in close proximity of conspecifics (Gursky, 2000b).

During the activity period, social interactions occurred regularly. Males generally had higher interaction frequencies than females and interacted more often with females than expected from their spatial overlap patterns. The observed interaction frequencies of 1–2 interactions per hour correspond to findings in other solitary primates (*Microcebus murinus*: Pagès-Feuillade, 1988; Schmelting, 2000; Radespiel, 2000b; *M. ravelobensis*: Weidt *et al.*, 2004; *Galago crassicaudatus*: Clark, 1985; *Tarsius spectrum*: Gursky, 2000b) but are much higher than in *Mirza coquereli* (Kappeler, 1997b), which interacted only once per 10 h.

Genetic Structure

Several aspects of the genetic population structure of Kirindy *Microcebus berthae* indicated a potential for female philopatry and male dispersal. First, the average relatedness among females in the population was higher than among males. Second, females had on average one close relative more in the population than males did. Only one female with a peripheral home range, but 2 males with central ranges, were without close kin. Third, among male dyads with spatial overlap there were fewer closely related dyads than among spatially separated dyads. However, our preliminary observations need to be confirmed in a larger sample, also determining mitochondrial DNA variability (Wimmer *et al.*, 2002; Kappeler *et al.*, 2002).

Our preliminary genetic results provided no indication for the existence of matrilineal lines. Dyads of spatially close or separated females did not differ in average relatedness, which also is true for the number of close relatives among them. Moreover, only 2 females with neighboring home ranges were potential mother-daughter/sister-pairs. Spatial clusters of closely-related females exist in other solitary cheirogaleids, e.g., *Mirza coquereli* (Kappeler *et al.*, 2002) and *Microcebus murinus* (Radespiel *et al.*, 2001; Wimmer *et al.*, 2002), and in some other mammals with female

philopatry, e.g., *Myotis bechsteinii* (Kerth *et al.*, 2000), *Clethrionomys rufocanus* (Ishibashi *et al.*, 1997) and *Lycaon pictus* (Girman *et al.*, 1997).

Several factors might have reduced the probability of detecting matriline in this study. First, generally there were few potential parent-offspring/sibling-pairs, which might be due to high population dynamics. Mouse lemurs have one of the highest mortality rates among primates: between 25%, (Goodman *et al.*, 1993) and 50% (M. Eberle, pers. comm.). Also, the assumed highly promiscuous mating system together with potential mixed paternities, as in *Microcebus murinus* (Radespiel *et al.*, 2002; Eberle and Kappeler, 2004b) and *Mirza coquereli* (Kappeler *et al.*, 2002) might reduce the number of full-siblings in the population (Worthington Wilmer *et al.*, 1994; Wimmer *et al.*, 2002). Moreover, members of matriline beyond first-degree relatives cannot be detected with microsatellite markers (Awise, 1994). Therefore, our preliminary findings should be complemented with data about observed dispersals and variability in mtDNA.

Mating System

Spatial Distribution

The spatial distribution of pygmy mouse lemurs revealed extensive intra- and intersexual home range overlap, which allows males and females potential access to more than 1 mating partner. Each female's home range overlapped with ≥ 8 males, but only with 1 or 2 other females. Male ranges encompassed those of 3–4 females but also those of ≤ 9 other males. In an extensive radio-tracking study of an almost completely known population of *Microcebus murinus*, Eberle and Kappeler (2001, 2002, 2004a, 2004b) found that males have spatial access to ≤ 21 females. Competition among gray mouse lemur males is intense because ≤ 14 other males were in the home range of one female and some females mated with ≤ 7 different males. In *Mirza coquereli*, male ranges overlapped with those of 4–15 females during the mating season (Kappeler, 1997b). High female dispersion due to large female home ranges and low population density in pygmy mouse lemurs might reduce the number of spatially accessible females per male.

Several indirect observations indicate that scramble competition is the main mechanism of male-male competition in pygmy mouse lemurs. First, males use home ranges about twice the size of female ranges, which has also been observed by Schwab (2000), in gray mouse lemurs (Pagès-Feuillade, 1988; Fietz, 1998, 1999a; Radespiel, 2000b; Eberle and Kappeler, 2002, 2004b) and in other solitary prosimians by Clark (1985) and Kappeler

(1997b) and in other mammals (Schwagmeyer, 1988; Gehrt and Fritzell, 1998). Second, in contrast to females, males expand their ranges during the mating season, a pattern also of other promiscuous or polygynous species (*Microcebus murinus*: Radespiel, 2000b; Eberle and Kappeler, 2004b; *Mirza coquereli*: Kappeler, 1997b; *Spermophilus tridecemlineatus*: Schwagmeyer, 1988; *Apodemus sylvaticus*: Tew and Macdonald, 1994; *Mustela erminea*: Erlinge and Sandell, 1986), resulting in improved access to additional potential mates. Third, males travel longer distances per night than females. High mobility of males within the mating season should enhance the chance to encounter receptive females. Accordingly, mobility is an indicator of scramble competition (*Microcebus murinus*: Schmelting, 2000; Eberle and Kappeler, 2004b; *Sorex araneus*: Stockley *et al.*, 1994; *Onychogalea fraenata*: Fisher and Lara, 1999). Thus, large male home ranges that provide spatial access to more than one female, maximization of ranges during the mating season, in combination with intensive roaming, enhances the chance for males to meet estrous females and to monitor their reproductive state by detecting olfactory and acoustic signals (Tew and Macdonald, 1994).

Sexual Dimorphism

Data about sexual dimorphism in *Microcebus spp.* are controversial. Some researchers found no difference between males and females (*Microcebus berthae*: Schmid and Kappeler, 1994; Schwab, 2000; *M. murinus*: Fietz, 1998; Schmid and Kappeler, 1998), whereas others described female-biased dimorphism in canine size and head length (*M. murinus*: Kappeler, 1990b, 1996, 1991; Jenkins and Albrecht 1991). In the study population, females had larger head widths and head-body-lengths than males. Captive gray mouse lemurs showed strong reversed sexual dimorphism in body mass with females being $\leq 21\%$ heavier than males (Young *et al.*, 1990; Kappeler, 1990b, 1991, 1993b; Jenkins and Albrecht, 1991). Field studies demonstrated different seasonal body mass development in males and females, leading to fluctuating sexual dimorphism (Fietz, 1998; Schmid and Kappeler, 1998; Schmid, 1999). Outside the mating season, females were heavier than males (reversed sexual dimorphism) and males were heavier than females during the mating season. The seasonal increase in male body mass, which also occurs in *Microcebus berthae*, is partly (*ca.* 30%) due to enlargement of the testes at the onset of the mating season (Schmid, 1997; Fietz, 1999a; Schwab, 2000), possibly fuelled by a continuous improvement of food availability in the transition from the cool dry season to the wet season (Martin, 1972; Hladik *et al.*, 1980).

Testicular Size

Compared to other mammals, male *Microcebus berthae* have relatively large testes (Kenagy and Trombulak, 1986; Schwab, 2000). With a mass of both testes between 3.6% (this study) and 4.3% (Schwab, 2000) of the body mass it is in fact the highest among all primates (Harcourt *et al.*, 1981; Kenagy and Trombulak, 1986; Kappeler, 1997a; Schwab, 2000) and is higher than expected for a strepsirrhine of this body mass (Kappeler, 1997a; Schülke *et al.*, 2004). Testicular size showed pronounced seasonal fluctuations with a 5-fold increase shortly before and within the short mating season, which also occurs in *Microcebus murinus* (Fietz, 1999a; Peters *et al.*, 2000; Schmelting, 2000) and in other solitary prosimians (*Galago moholi*: Pullen *et al.*, 2000; *Mirza coquereli*: Kappeler, 1997b). If estrous females mate with more than 1 male, postcopulatory mechanisms such as sperm competition and mate-guarding become increasingly important in male-male competition (Parker, 1970; Curtsinger, 1991; Birkhead and Parker, 1997). Thus, a high relative testicular volume is typical for species with pronounced competition between male ejaculates (Harcourt *et al.*, 1981; Kenagy and Trombulak, 1986; Schulte-Hostedde and Millar, 2004).

Estrous Synchrony

All trapped females came into estrous within 10 days, so that reproduction was highly seasonal (see also Petter *et al.*, 1977; Tattersall, 1982; Pereira, 1991; Richard and Dewar, 1991; Mittermeier *et al.*, 1994; Eberle and Kappeler, 2002; Schülke, 2003). We were able to trap several females more than once during reproductive activity, which allowed a preliminary analysis of the temporal distribution of estrus in the population. In a given night, only one or a few females were actually receptive, resulting in weak estrous synchrony. In a detailed study of spatial and temporal distribution of fertile females, Eberle and Kappeler (2002, 2004a) also detected no synchrony in *Microcebus murinus* within a short annual mating season (see also Radespiel and Zimmermann, 2000, and Pereira, 1991 for *Lemur catta*). Since the temporal distribution of female receptive periods is a main determinant of the operational sex ratio and thus a key factor affecting male monopolizing potential, our preliminary results indicate that males should in principal be able to monopolize estrous females.

SOCIAL STRUCTURE

Describing the social structure of small, cryptic nocturnal primates is challenging. Field studies of the last 3 decades have demonstrated that

many of the solitary foragers live in elaborate social networks based on regular sleeping associations and social interactions (Martin, 1972; Clark, 1985; Harcourt and Nash, 1986; Bearder, 1987; Warren and Crompton, 1997; Radespiel *et al.*, 1998; Gursky, 2000b). Intensive focal observations revealed that many of the cryptic species meet during nocturnal activity and show great diversity of social behavior (Clark, 1985; Pagès-Feuillade, 1988; Warren and Crompton, 1997; Gursky, 2000b, 2002).

Our results indicate that the social structure of *Microcebus berthae* is similar to that of other mouse lemurs. We observed inter- and intrasexual social interactions of affiliative, affiliative and agonistic character throughout the night, also outside the mating season. Long huddling and grooming bouts between sleeping group members at the onset and at the end of the nightly activity period were common. In general, the social behavior of *Microcebus berthae* is diverse, ranging from huddling and grooming to chasing each other and fighting; it accounted for *ca.* 7–8% of the activity budget. Agonistic interactions occurred in feeding and sexual contexts. All intersexual conflicts were won by females, which indicates female dominance. Also, captive female gray mouse lemurs decided nearly 100% of conflicts in their favor (Radespiel, 2000a; Radespiel and Zimmermann, 2001). In contrast to most other primates and mammals, females are dominant over males or have feeding priority in many lemur species (Ralls, 1976; Hrdy, 1981; Jolly, 1984; Pereira *et al.*, 1990; Kappeler, 1990a, 1993a; Schülke and Kappeler, 2003; Pochron *et al.*, 2003), but the evolutionary roots and function of this lemur idiosyncrasy remain in the dark.

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