First Insights into the Social Organisation of Goodman's Mouse Lemur (*Microcebus lehilahytsara*) – Testing Predictions from Socio-Ecological Hypotheses in the Masoala Hall of Zurich Zoo

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Key Words

Social interaction · Spatial distribution · Sociality · Sleeping group · Genetic relatedness · Lemurs · Solitary forager · Strepsirhines

Abstract

Following current socio-ecological hypotheses, the social organisation of a species is mainly determined by resource quality and distribution. In the case of *Microcebus* spp., a taxon-specific socio-ecological model was formulated earlier to explain their variable social organisation. The aim of this study was to test predictions from this model in Goodman's mouse lemur based on a data set from animals living in the semi-free colony of Zurich Zoo. During a 2-month study, we observed 5 females and 5 males using radiotelemetry. We collected data on space use and social behaviour, on sleeping sites and on sleeping group composition. Predictions were only partly confirmed. As expected, Goodman's mouse lemurs were solitary foragers with an increased level of sociality due to crowding effects at the feeding stations. In contrast to the prediction, females and males formed unisexual sleeping groups, which were stable in females and of a fission-fusion type in males. Whereas the formation of sleeping groups by both sexes may be triggered by thermoregulatory benefits, the formation of unisexual sleeping groups may result from divergent interests of the sexes. We conclude that the existing model for the evolution of mouse lemur social organisation needs to be refined.

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Introduction

Following basic socio-ecological hypotheses, the social organisation of a species is mainly determined by resource quality and distribution as well as predation [Crook and Gartlan, 1966; Emlen and Oring, 1977; Terborgh and Janson, 1986;

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Sterck et al., 1997]. They assume that the distribution of individuals depends on sex-specific resources that mainly determine their biological fitness. Thus, they predict that female distribution and their degree of sociality is mainly influenced by the distribution and quality of food and shelter [Crook and Gartlan, 1966; Emlen and Oring, 1977; Terborgh and Janson, 1986], whereas male distribution mainly depends on that of receptive females [Altmann, 1990]. Testing these predictions in taxa (e.g. genera) with high species diversity will help to identify the underlying mechanisms that contribute to diverse social traits, since phylogenetically confounding factors are greatly reduced. At the same time, hypotheses can be expanded and refined by including taxon-specific factors [Janson, 2000].

The infraorder Lemuriformes includes 5 families and these families contain many diverse species. The current knowledge of their social organisation suggests that high social variability can occur even within one genus. One example is *Microcebus*, which currently consists of 19 described species [Mittermeier et al., 2010; Radespiel et al., 2012]. Detailed observational studies on the social organisation of mouse lemurs have been conducted on only 4 of these species, all of which inhabit the western lowland dry forest habitats (*Microcebus murinus* [Radespiel, 2000; Ebnerle and Kappeler, 2002, 2006; Dammhahn and Kappeler, 2009]; *M. ravelobensis* [Weidt et al., 2004]; *M. berthae* [Dammhahn and Kappeler, 2005, 2009]; *M. griseorufus* [Génin, 2008]). Previous studies described mouse lemurs as solitary foragers, forming sleeping associations during the daytime, which appears to be the basic social unit in these species. However, even among these few species, differences concerning the proportion of home range overlap between females, the number of females that share home ranges and the composition and temporal stability of sleeping groups can be found [reviewed in Radespiel, 2006].

Schülke and Ostner [2005] formulated a socio-ecological model (Schülke-Ostner SEM) for evolution of the social organisation within the genus *Microcebus* based on previous general socio-ecological hypotheses. They hypothesized that several factors, such as the potential for cooperative breeding and the quality of sleeping sites, should lead to different social systems. For example, high population density should lead to the establishment of female-female associations which can take the form of all-female groups (+solitary males) or of multi-male multi-female groups, depending on the quality (safety and insulation capacity) of sleeping sites. The Schülke-Ostner SEM was developed on the basis of field studies conducted on mouse lemur species from different western lowland dry forest habitats. Since mouse lemurs also occur throughout the eastern Malagasy rain forests and these species differ strongly in their ecology, it is of special interest to know whether the model can also explain the social organisation of rain forest species. Due to a lesser degree of rainfall seasonality in rain forests [Randrianambinina et al., 2003], food abundance should not vary to the extent known in dry forests [Dammhahn and Kappeler, 2008; Thorén et al., 2011]. Instead, thermoregulation could play at least a similar role, since highland rain forest habitats can reach very low minimum temperatures during the austral winter. Thus, relatively lower feeding competition and the need for partners to benefit from social thermoregulation [Perret, 1998] could potentially promote a higher degree of sociality in both sexes in rain forest species.

Our goal was to test predictions that can be derived from the Schülke-Ostner SEM for the spatial and social structure in a semi-free living Goodman's mouse lemur population (*Microcebus lehilahytsara*). Goodman's mouse lemur was previously

considered to be *Microcebus rufus* but was described as a separate species in 2005 [Kappeler et al., 2005]. Its natural habitats are the highland rain forests of central-eastern Madagascar. So far, only sparse data about its ecology and social organisation are available from the field. Preliminary investigations provided first evidence of unisexual sleeping groups that were composed of 2–4 individuals [Randrianambinina, 2001].

The rain forest hall of Zurich Zoo offers the unique opportunity of a semi-free setting in which some factors that should contribute to the social organisation of Goodman's mouse lemurs, such as food distribution, animal density or predation, are well known or controlled for. The climatic conditions in the hall depend on the weather outside, but temperatures are usually kept between 24 and 34°C in the daytime and cool down to a minimum of 18°C at night. The yearly light regimen follows the natural photoperiod of Zurich, since the walls of the hall are transparent. Occasional artificial rain from a sprinkler system waters the plants during the night. Altogether, the climatic conditions in the hall generally reflect well the conditions known from free-living Goodman's mouse lemurs [Randrianambinina et al., 2003] but lack some extremes, e.g. in monthly minimum temperatures and in the maximum amount of rainfall per month. During the winter months, Goodman's mouse lemurs in the hall stop visiting the feeding stations and are assumed to enter prolonged torpor, although provision continues [Zurich Zoo, unpubl. data]. The existence of seasonal torpor, which has also been observed in the wild [Randrianambinina et al., 2003], indicates that the animals suffer from the relatively low temperatures in the hall and should benefit from good insulation in high-quality sleeping sites like tree holes [Schmid, 1998]. Due to the young age of the plants in the Masoala hall, however, there are no such holes available. Other shelters have therefore to be used, and social thermoregulation should gain importance under these conditions [Perret, 1998].

Based on the Schülke-Ostner SEM, we derived several predictions for the social organisation of the Goodman's mouse lemurs in the hall. First, the animals should in principle forage solitarily like all previously studied mouse lemur species [summarised in Radespiel, 2006]. However, in the absence of predation and under ad libitum food supply, we predicted a higher degree of sociality, i.e. longer times spent in proximity to conspecifics. Third, social interactions should be more often neutral or affiliative compared to free-living mouse lemurs. Fourth, due to the relatively high population density in the restricted area of the hall and a predisposition for cooperative breeding [Schülke and Ostner, 2005], we predicted the existence of stable female-female associations. Given the presumably low quality of sleeping substrates in the hall, these associations should take the form of multi-male multi-female groups rather than all-female groups and solitary males [Schülke and Ostner, 2005].

We tested these predictions by investigating the spatial and social structures formed by 10 radio-collared individuals in the Masoala hall. We determined and compared male and female home ranges and overlaps, the degree of proximity and genetic relatedness, social interactions between the animals, and the composition and stability of sleeping groups. Furthermore, we collected data about sleeping site substrates and usage frequencies to characterize their quality.

Methods

Study Site and Study Period

The study site was the Masoala hall of Zurich Zoo, Switzerland (8.57° E, 47.38° N, approx. 600 m above sea level). The Masoala hall is 1.1 ha in size and contains more than 3,400 individual plants, 42 vertebrate species, and numerous arthropod species. The vertebrates in the hall are individually marked with a subcutaneous transponder chip (ID-100, Trovan Unique™).

In 2005, 6 wild-caught male and 1 wild-caught female Goodman's mouse lemurs, originating from the Andasibe region in Eastern Madagascar, were introduced into the hall. One year later they had already reproduced successfully. Three more females from the University of Veterinary Medicine Hanover were introduced in 2007. Since then, the population has grown rapidly. As of May 2010, a total of 51 mouse lemurs have been individually marked with transponders.

The Goodman's mouse lemurs are fed with a fruit mix every night at two feeding stations that are positioned at opposite sides of the hall (fig. 1a). The feeding stations consist of a cage that the mouse lemurs can enter and leave through a tube which is equipped with a transponder reading device (LID 665, Trovan Unique™). Thus, the feeding visits of all marked mouse lemurs are monitored continuously by the zoo management, facilitating the estimation of the actual population size and of seasonal torpor. Of the original 51 marked individuals, 20 females and 17 males regularly visited the feeding stations in May 2010. In addition to provisioning, the mouse lemurs could feed opportunistically on plant or animal matter in the hall.

Most Goodman's mouse lemurs stop visiting the feeding stations during winter time and undergo prolonged seasonal torpor. In the years 2008–2010, most mouse lemurs started activity again between the end of February and the end of March [Zurich Zoo, unpubl. data]. The study period ranged from the beginning of March to the end of May 2010. When our observations started on March 22, 2010, 13 of 37 mouse lemur individuals were recorded at the feeding stations and therefore assigned as active.

Capture and Marking

The first 2 weeks of the study period were used as an orientation phase in order to learn about the paths, animals and plant species in the hall. Accordingly, we trapped mouse lemurs between March 17 and 31, 2010, to equip 10 individuals with radio collars. During one capture night, we set up 5–6 Sherman live traps (7.62 × 8.89 × 22.86 cm), each baited with a piece of banana, between 17.00 and 0.00 h in each of the two non-provisioned feeding stations. We identified a captured mouse lemur with a portable transponder chip reader (ISO MAS III, Datamars, Switzerland) and transferred it to a transparent plastic box (15 × 30 × 20 cm, prepared with holes to allow circulation) that contained some food and water as well as one dark plastic tube for retreat. Captured mouse lemurs were anaesthetised the next morning with isoflurane gas. Small ear biopsies were taken from each individual for genetic analyses. For better identification of the sexes during nightly observations, all animals got sex-specific shave marks on their tail. We equipped 5 males and 5 females with radio collars (1.5 g, PIP 3, Biotrack, UK). Radio-collared individuals will hereinafter be termed focal animals.

After handling, we transferred all animals back to their plastic box with paper towels inside to guarantee a gentle awakening from anaesthesia. Within a few minutes, they woke up and retreated into the dark plastic tube. One to 2 h after that we transported them back to the hall and placed them into the feeding stations. We opened the box lids but most animals stayed in the dark plastic tubes and slept there until dusk. After the last observation night, we repeated capture procedures to remove all radio collars from the focal animals.

Focal Observations and Sleeping Site Patrols

The hall is partitioned by the zoo management into 72 grid cells (fig. 1) that were also used for data collection. For nightly observations, we used the visitors' and zookeepers' paths and a path of approximately 1 m width directly along the outer edges.

During the first week of observations, we observed 2 males, once from 19.00 to 0.00 h and once from 0.00 to 6.00 h, in order to explore general differences in behaviour between the first

Fig. 1. **a** Map of the Masoala hall of Zurich Zoo; thin light grey lines = grid cell boundaries; light grey areas = water and marsh areas; dark grey lines = pathways; FS = feeding stations for Goodman's mouse lemurs. **b–k** Small maps of the hall showing individual home ranges (grey areas) of males (**b–f**) and females (**g–k**) and their sizes in hectares.

and the second half of the night. Both animals fed repeatedly at the feeding stations throughout the night. The transponder readers at the feeding stations confirmed this general observation for the rest of the population. The opportunity to observe social behaviour was however higher in the first half of the night. In addition, the two animals showed a higher frequency of locomotion, resulting in lower contact times with the observer, during the second half of the night. For these reasons we performed all other observations in the 4 h following first visual contact at the

Fig. 1. b–k Small maps of the hall showing individual home ranges (grey areas) of males (**b–f**) and females (**g–k**) and their sizes in hectares.

sleeping site at dusk. Consequently, observations started between 19.00 and 20.00 h and ended between 23.00 and 0.00 h, European winter time.

We observed each individual with the help of head lamps and a MagLite torch during 4 different half nights in total. We recorded all data on a digital voice recorder (WS-321M, Olympus, Germany). For the observations we used a randomized block design with 4 blocks of 5–15 half nights each. In the first block with 5 observation nights (from March 22 to 26, 2010) we observed only males, since females had not yet appeared at the feeding stations. We recorded the first female on March 24, 2010. After capturing and collaring the females, the second ob-

servation block started (15 half nights). In this block, we observed each male once, whereas we observed each female twice. The following 2 observation blocks contained 10 half nights each in which we observed each individual once.

During the study period, we determined on a daily basis the sleeping sites of the focal animals as well as the plant species slept in. We estimated sleeping group size by counting the non-collared co-sleepers of the focal animal when they left the sleeping site at the beginning of the nocturnal observations. During observations, we followed the focal animal using a receiver (Sika, Biotrack, UK; antenna: Model RA-14, Telonics, USA) and recorded movements by noting every change between grid cells continuously during contact time. We furthermore recorded all social encounters, social behaviours during encounters, and their locations continuously using behaviour sampling [Altmann, 1974]. We defined social encounters as situations in which at least one other mouse lemur was in proximity of up to 2 m to the focal animal. By definition, whenever an individual entered or left this 2-metre radius, the previous encounter ended and a new encounter started, if there was still at least 1 individual left in proximity to the focal individual. Short episodes of dyadic agonistic interactions were defined as conflicts. The decision and optionally the identity and sex of the winner of a conflict were determined if possible following Pereira and Kappeler [1997].

Laboratory Procedures

We extracted DNA from 45 individuals (24 males, 21 females) from tissue biopsies ($n = 25$) by a phenol-chloroform protocol [Sambrook et al., 1989] and/or from plucked hairs ($n = 20$) as described earlier [Radespiel et al., 2009]. Samples had been collected either as part of this study ($n = 24$) or during earlier yearly routine capture zoo sessions ($n = 21$). We amplified 5 nuclear microsatellite loci that have been characterised previously (Mm3, Mm8, Mm10 [Radespiel et al., 2001a]; Mm30 [Hapke et al., 2003]; Mm9n [Radespiel et al., 2008]). We performed primer-specific PCRs in a total volume of 10 μ l (msat loci) according to the protocols provided in Radespiel et al. [2008]. Fragment lengths were determined either by running PCR products on a MegaBACE™ 1000 or on an ABI 3500 capillary sequencer. Genotypes were determined either with the software Genetic Profiler 2.2 (MegaBACE data set) or with Genemapper 4.1 (ABI3500 data set). Compatibility of the two data sets was secured by running a subset of samples on both capillary sequencers. In total, 438 alleles were genotyped and assigned to the 45 individuals (missing alleles: 2.2%). The numbers of alleles per locus ranged from 7 (Mm30) to 15 (Mm8, Mm9n), the mean allelic richness was 10.55, and the probability of identity was $<10^{-6}$ [Botstein et al., 1980].

Data Analysis

We calculated home range sizes by summing up the size of individual grid cells used during nightly observations. In order to compare different home range overlap proportions, we calculated an overlap index for each of the 45 possible dyads of the focal animals following Lazo [1994]:

$$\text{overlap index} = 2 \times (\text{area}_{ab}) / (\text{area}_a + \text{area}_b),$$

where area_{ab} = home range overlap area of individuals a and b, area_a = home range area of individual a and area_b = home range area of individual b. The overlap index can range from 0 (no overlap) to 1 (100% overlap).

In addition to counting sleeping group members at dusk, we identified sleeping groups during daily sleeping site controls of the focal animals. We calculated the genetic relatedness (r-value) among all members of the population according to the procedures described by Radespiel et al. [2001b, 2003]. Based on this data set, the r-values of cosleeping and non-cosleeping focal animals were compared.

Preference indices were calculated for each plant species that was used as a sleeping substrate. For this calculation, the number of observed usage days (animals $\times$ days) was divided by the expected number of usage days for each plant species that was used as sleeping substrate. The expected number of usage days was calculated for each plant species as

$$N_{e\text{-usage}} = (N_a / N_{\text{total}}) \times N_{\text{focal}} \times D,$$

where N_a = number of plant specimens of species *a* in the hall, N_{total} = total number of plant specimens of all plant species used as sleeping sites in the hall, N_{focal} = number of focal animals, and D = number of days with sleeping site controls.

This preference index was calculated for 8 out of 10 observed sleeping site plant species. For the 2 others (*Schizostachyum brachycladum*, *Asparagus falcatus*), the exact number of plant specimens in the hall was not known. Return days were defined as the number of consecutive observation days during which an individual used the same sleeping site as the day before.

Statistical Procedures

We performed all comparisons between the sexes as well as between cosleeper and non-cosleeper dyads with non-parametric Mann-Whitney U tests. The Wilcoxon matched-pairs test was used to compare the number of conflicts won by males and females. The relationship between the degree of relatedness (*r*-value) and percentage of days with shared sleeping site was tested with the Spearman rank correlation coefficient. All statistical tests were 2-tailed with a significance level of $p < 0.05$ and were performed with Statistica 6.1 (StatSoft Inc., USA).

Ethical Note

All research procedures adhered to the legal requirements of Switzerland and conformed to the ethical standards of the Association for the Study of Animal Behaviour.

Results

Contact Time

Contact time (time of visual contact by the observer of the focal animal) was limited by vegetation and path restrictions and varied individually and nightly with an average total contact time of 5.7 h/animal (range: 2.1–9.8 h/animal) which accounts for 35.3% (range: 13.4–60.7%) of individual observation time. There was no significant difference in individual total contact time between the sexes (Mann-Whitney U test: $Z = -0.31$, $p = 0.841$, $n = 5$ males/females).

Home Ranges and Their Overlap

All female home ranges were smaller than all male home ranges (Mann-Whitney U test: $Z = 2.61$, $p = 0.008$; fig. 1b–k). Male home ranges were on average 4 times larger (median: 0.58 ha) than female home ranges (median: 0.14 ha). Male home ranges were overlapped by individual female home ranges to a relatively small proportion (median: 11%, range: 0–34%). In contrast, female home ranges were often overlapped by individual male home ranges to a larger extent (median: 51%, range: 0–90%). There was a trend for a sex difference in overlap indices (Mann-Whitney U test: $Z = 1.74$; $p = 0.089$; $n = 10$ male – male/female – female dyads). Intrasexual overlap indices between males were medium-sized to large (range: 0.29–0.81; fig. 2) and had a unimodal distribution, reminiscent of a normal distribution. In contrast, home range overlap indices between females had either very high or very low values (range: 0–0.91) and therefore had a bimodal distribution. Overlap indices of female cosleepers were significantly higher than overlap indices of female non-cosleepers (Mann-Whitney U test: $Z = -2.47$, $p = 0.017$, $n = 3$ cosleeper dyads, $n = 7$ non-cosleeper dyads; fig. 2).

Usage of Feeding Stations

Focal males and females used the feeding stations nearly every night. Females did not switch between the two stations but used only one of them during the whole

Fig. 2. Home range overlap indices of cosleeping and non-cosleeping male-male and female-female dyads (explanations in the text).

observation period. In contrast, focal males switched between the feeding stations 12–33 times with a median of 14 times during the study period of 62 nights. Males used both feeding stations in 1 night during 8–23% of the nights with a median of 9%.

Social Encounters

The mean proportion of contact time spent in proximity to at least 1 other mouse lemur was 38% (range: 19–73%). If the time near a feeding station is subtracted, the mean time in proximity decreased to 14% (range: 3–49%). Encounters ($n = 626$) occurred with a median of 10 times/h (range: 5–21 times). On average, 75% of individual encounters (range: 61–82%) took place without any further social interaction between the encounter partners. Agonistic behaviours occurred during most encounters with social interactions (130–186 encounters), and this was true for both sexes (median_{males}: 80%; range: 60–100%; median_{females}: 76%; range: 64–84%). Fifty-one percent of all conflicts (73 of 144 conflicts) occurred in the feeding context. In general, females won intersexual dyadic conflicts more often than males (total won by females: 65, total won by males: 4; Wilcoxon matched-pairs test: $Z = 2.80$, $p = 0.005$, $n = 10$). Four focal animals never showed affiliative behaviours. However, 1 female (F3) showed affiliative behaviour in 52% of her encounters with social interactions (17 of 33 encounters). The relative proportion of encounters with agonistic and affiliative interactions did not differ between the sexes (Mann-Whitney U test: $Z_{\text{affiliative}} = -1.19$, $p = 0.310$, $n = 5$ males/females; $Z_{\text{agonistic}} = 0.52$, $p = 0.690$, $n = 5$ males/females).

Sleeping Group Composition

The sleeping groups that were determined at the beginning of the evening observation were typically composed of either males or females ($n = 31$), whereas

Table 1. Days spent together in one sleeping site, genetic relatedness and total number of observed days

	M1	M2	M3	M4	M5
M1		-0.21	0.01	-0.04	-0.22
M2	10		-0.26	0.24	0.45
M3	15	2		-0.24	0.15
M4	8	15	2		-0.03
M5	11	12	16	4	
T	33	37	47	35	41
	F1	F2	F3	F4	F5
F1		-0.10	-0.13	-0.32	-0.17
F2	0		0.15	0.53	0.23
F3	0	0		0.46	0.10
F4	0	36	0		0.57
F5	0	33	0	34	
T	43	43	38	41	40

Upper matrix values: genetic relatedness (r-values, according to Queller and Goodnight [1989]); lower matrix values: days spent together in one sleeping site. M1–M5 = male 1 to male 5; F1–F5 = female 1 to female 5; T = total number of observed days.

mixed-sex groups ($n = 4$) were as rare as solitarily sleeping individuals ($n = 5$). The average group size was 3 individuals and the maximum was 6 for both sexes. Once, a mixed-sex group of 7 members (4 females, 1 male and 2 animals of unknown sex) was detected.

The sleeping group composition could be determined on 33–47 days per focal animal (table 1). Focal males did not form stable sleeping groups. However, each individual shared a sleeping site at least twice with every other focal male but never with one of the focal females. Some male dyads shared a sleeping site more often than others. For males the percentage of days spent together in one sleeping site was significantly and positively correlated with genetic relatedness (r-value, Spearman rank correlation: $R_s = 0.79$, $p = 0.006$, $n = 10$; table 1). Male dyads that had an r-value ≤ 0 (i.e. unrelated) slept together on 0–30% of the observation days, whereas male dyads with an r-value > 0 shared the sleeping site on 31–42% of the observation days.

In contrast to male grouping patterns, 3 of the 5 focal females (females F2, F4 and F5) belonged to one stable sleeping group consisting of 4–7 members in total. These 3 females were found together during 33–36 days (80–95% of observation days; table 1). The other 2 focal females belonged to different groups containing 2–6 unknown members, respectively. The r-values of female dyads belonging to the stable sleeping group were significantly higher than those of non-cosleeping dyads (Mann-Whitney U test: $Z = -2.17$, $p = 0.033$, $n = 3$ cosleeper dyads, 7 non-cosleeper dyads). It is known that females F4 and F5 are full sisters, descending from different litters

Fig. 3. Preference indices of sleeping site plant species (explanations in the text).

of the breeding colony at the University of Veterinary Medicine, Hanover. The r -values and the results of a parentage analysis (results not shown) suggest that female F2 is the daughter of female F4 ($r_{F4/F5} = 0.57$; $r_{F2/F4} = 0.53$; $r_{F2/F5} = 0.23$; table 1).

Usage of Sleeping Sites

Sleeping sites were distributed across the whole hall. Forty-four sites were found and in 33 cases (75%) the plant species could be identified. The identified sites can be best characterised as leaf structures, often situated close to the trunk (e.g. dead leaves hanging down the trunk in several layers in the case of *Pandanus* spp.). Tree holes were not identified. Sleeping sites were found in 10 different plant species [for species names, see fig. 3, *S. brachycladum* ($n = 2$), *A. falcatus* ($n = 1$)]. Fifty-two per cent of the sites ($n = 23$) were trees of the genus *Pandanus* belonging to *P. baptistii* ($n = 7$) and *P. utilis* ($n = 13$) or to an undetermined *Pandanus* species (fig. 3). Pooling the daily sleeping site usage data of all focal animals revealed that *Pandanus* sp. was used in 85.9% of all cases ($n = 467$). *P. baptistii* was used over 5 times more often than expected on the basis of its relative availability in the hall (fig. 3). Together, the 3 used *Pandanus* species had an overall preference index of 3.31 and were therefore used about 3 times more often than expected. Males used more different sleeping sites per month (median: 8, range: 6–12) than females (median: 3, range: 2–6; Mann-Whitney U test: $Z = 2.4$, $p = 0.016$, $n = 5$ males/females) and they had a lower number of return days (median: 2, range: 1–3) than females (median: 6, range: 3–13; Mann-Whitney U test: $Z = -2.4$, $p = 0.016$, $n = 5$ males/females).

Discussion

Spatial Structure

Space use of Goodman's mouse lemurs in the Masoala hall of Zurich Zoo was not strikingly different from the preliminary data set available from the wild. Individuals did not use the whole hall but instead established a complex spatial structure. Male total home ranges (0.37–0.63 ha) were slightly bigger than those found in a preliminary study on free-living male Goodman's mouse lemurs during the mating season (0.22–0.42 ha, $n = 3$ [Randrianambinina, 2001]). In contrast, female home ranges were found to be smaller in this study (0.09–0.18 ha) compared to 0.21–0.3 ha in the wild ($n = 3$ [Randrianambinina, 2001]). A plot depicting the increase in female home range grid cells against increasing observation time delivered an asymptotic curve which reached its plateau after the second half night (results not shown), suggesting that the difference in spatial requirements between captive and free-living females may not be based on the limited observation time. Instead, the difference is probably due to captive space constraints and a high animal density, combined with a centralised food provisioning regime.

In contrast to males, each focal female used only 1 of the 2 feeding stations during the whole study period. Transponder data from previous years confirm this high fidelity of females towards 1 of the 2 feeding stations [Zurich Zoo, unpubl. data]. This suggests that if sufficient food resources are available, there seems to be no need for females to enlarge their home ranges further. A study on free-living female Madame Berthe's (*M. berthae*) and grey mouse lemurs (*M. murinus*) showed that this effect can also be observed under natural conditions [Dammhahn and Kappeler, 2009]. Females of both species reduced their home range size on average to 50% when artificial feeding stations were added to their natural environment [Dammhahn and Kappeler, 2009].

Male home ranges in the hall were on average 4 times larger than female home ranges and included both feeding stations. The sex difference in our preliminary data may be either the result of a sex-specific feeding strategy or male roaming behaviour. The observation that females won more conflicts than males suggests that females might have been dominant over males. Males may therefore have benefitted energetically if they switched between the feeding stations opportunistically. However, males did not typically use both feeding stations in one night. Therefore, it is unlikely that the large home ranges were needed to fulfil the males' nutritional needs. The data rather suggest that males were roaming in search of receptive females, since both feeding stations were regularly visited by females, and it should thus be advantageous for males to patrol both feeding stations more or less frequently. Male roaming behaviour has been shown in other *Microcebus* species under free-living conditions (*M. murinus* [Radespiel, 2000; Eberle and Kappeler, 2002]; *M. ravelobensis* [Weidt et al., 2004]; *M. berthae* [Dammhahn and Kappeler, 2005]).

Sociality

We predicted a higher level of sociality in the semi-free setting compared to field studies due to the absence of predators and nearly unlimited food supply. Indeed, the average time in proximity to conspecifics (38%) and the encounter frequency (10/h) was high, when compared to other nocturnal lemurs with a dispersed social system (e.g. *Mirza coquereli*: 0.7/h [Kappeler, 1997]; *Phaner pallescens*: 2.3/h [Schülke and

Kappeler, 2003]). However, encounters with social interactions accounted for only 25% of all encounters, which is comparatively low [Génin, 2010].

Interestingly, affiliative behaviour was only rarely observed, whereas the majority of interactions involved agonistic behaviour, with most conflicts occurring in feeding contexts. Although this strong indication of feeding competition is unexpected given the unlimited food supply, it can be explained in view of the spatial setting in the hall. Encounters and a certain level of crowding at the feeding stations are unavoidable, since all 37 known population members are likely to have searched for food in 1 of the 2 feeding stations directly after waking up at dusk. The findings demonstrate that a clumped distribution of food resources, although provisioned ad libitum, can lead to severe food competition between individuals. Similar results were found in experimental studies on bonnet and rhesus macaques [Ram et al., 2003; Chancellor and Isbell, 2008]. On the basis of these and our findings, we would recommend having more than 2 feeding stations for 37 individuals. These feeding stations should be distributed over the whole hall to avoid crowding and accompanied conflicts.

If the times close to the feeding stations were excluded, proximity to other individuals dropped to 14% of total contact time which is similar to that found for grey (11%) and golden-brown (15%) mouse lemurs under free-living conditions (*M. murinus* [Pagés-Feuillade, 1988]; *M. ravelobensis* [Weidt et al., 2004]). These results show that cohesion was not continuous during the active time, although population density (≥ 33.6 individuals/ha) was strikingly higher than in the wild (*M. murinus*: < 5.3 , *M. ravelobensis*: < 9.3 [Rakotondravony and Radespiel, 2009]). The findings underline the dispersed nature of the social organisation of this mouse lemur species and their correct classification as solitary foragers.

Female Grouping Pattern

In accordance with our prediction we found evidence of female-female associations; however, they took the form of stable female sleeping groups consisting of matrilinear relatives that also shared large parts of their home ranges. From the female perspective, this social structure resembles that of the grey mouse lemur, in which females also form stable exclusive matrilinear sleeping groups [Radespiel et al., 2001b; Eberle and Kappeler, 2006; Lutermann et al., 2006]. Stable female sleeping groups were previously argued to be advantageous in the reproductive context (communal breeding) and for better resource acquisition (food and shelter) (*M. murinus* [Eberle and Kappeler, 2006, Lutermann et al., 2006]; *M. griseorufus* [Génin, 2010]). As food acquisition can probably be excluded as a selective pressure in the Masoala hall, female communal breeding is likely to also be an important driver of Goodman's mouse lemur sociality.

However, given the rather basic nature of the shelters used (leaf structures), the exclusivity of female groups is surprising and contradicts our prediction of multi-male multi-female groups [Schülke and Ostner, 2005]. It is possible that the insulation properties of the multi-layer dead leaves of the frequently used *Pandanus* sites are higher than previously thought. However, we would then expect males to sleep alone [Schülke and Ostner, 2005] due to the elevated level of intrasexual competition during the mating season. Alternatively, even if the low insulation properties of leaf shelters affect both sexes, a segregation of the sexes in separate sleeping groups could still be advantageous, since the particular interests of both sexes may be quite different (see below).

Male Grouping Pattern

In contrast to the prediction from the Schülke-Ostner SEM [2005] but in accordance with the preliminary data set from the wild [Randrianambinina, 2001], we found evidence for the regular formation of unisexual male sleeping groups in *M. lehilahytsara*. In contrast to females, however, male sleeping group composition was unstable over time: each focal male shared sleeping sites at least twice with every other focal male, but the number of shared days varied greatly from 2 to 16 days and correlated with the degree of relatedness between the males. These findings suggest a fission-fusion sleeping mode of male group members, and at present it cannot even be decided how many more males of the population were part of this multi-male sleeping network. Unstable primate groups can be regarded as a response to the costs of stable grouping [Lehmann et al., 2007]. In this case, costs could comprise the energetic costs of finding all group members at dawn [Braune et al., 2005], given the relatively large spread of the individual male home ranges. Indeed, male Goodman's mouse lemurs could save energy by using a nearby sleeping site at dawn and by joining with those familiar males that are close by.

The influence of genetic relatedness on grouping pattern remains puzzling, but the selectivity in the choice of cosleepers suggests some mechanism of kin recognition in male Goodman's mouse lemurs. Male sleeping groups have previously been reported in *M. berthae* and *M. griseorufus*. Whereas male groups were only found occasionally in *M. berthae* [Dammhahn and Kappeler, 2005], *M. griseorufus* forms stable and unisexual pairs on a regular basis that sometimes unite to larger associations, consisting of up to 3 pairs [Génin, 2008, 2010]. Neither the Goodman's type nor these two types of sleeping groups are satisfactorily explained by the Schülke-Ostner SEM for *Microcebus* [Schülke and Ostner, 2005].

Implication for Mouse Lemur Social Evolution

The Schülke-Ostner SEM [2005] can explain some aspects of the social organisation of Goodman's mouse lemur but not all characteristics. In agreement with the model, Goodman's mouse lemurs showed dispersed foraging activities with an increased level of sociality due to crowding effects close to the two feeding stations. Second, the distribution of females could be explained by the distribution of food resources, whereas males extended their activities widely beyond the proximity of the feeding stations, probably in order to localize receptive females [Eberle and Kappeler, 2004a]. Third, in accordance with the prediction under high population density, female-female associations (sleeping groups) were found, but in contrast to the Schülke-Ostner SEM for low-quality sleeping sites [Schülke and Ostner, 2005], the animals did not form multi-male multi-female groups but instead unisexual male and female groups.

Since segregation of the sexes in different sleeping groups has also been observed in the wild and in *M. griseorufus* [Randrianambinina, 2001; Génin, 2010], it seems to reflect a different route to sociality in the genus as a whole. The results from this study further suggest that the segregation of the sexes may reflect divergent interests of the sexes at least during this time of the year (early mating season [Eberle and Kappeler, 2004b]). Both males and females share the benefits of improved thermoregulation of sleeping groups, but differ in other adaptive advantages of group sleeping, i.e. communal breeding versus search for mates. Since these considerations should in principle be applicable to other mouse lemur species as well, it becomes

questionable whether stable multi-male multi-female groups can be expected in any mouse lemur species. Mixed-sex groups have so far been observed in *M. ravelobensis* [Weidt et al., 2004] and occasionally in *M. berthae* [Dammhahn and Kappeler, 2005], but a subsequent study revealed at least for *M. ravelobensis* that they can be best described as maternal rearing groups [Radespiel et al., 2009] and not as multi-male multi-female breeding groups.

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