ORIGINAL ARTICLE

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Spacing and group coordination in a nocturnal primate, the golden brown mouse lemur (*Microcebus ravelobensis*): the role of olfactory and acoustic signals

Abstract In order to remain stable, dispersed social groups have to solve two fundamental problems: the coordination of movement and cohesiveness within a group and the spacing between the groups. Here, we investigate mechanisms involved in intra-group coordination and inter-group spacing using the golden brown mouse lemur, *Microcebus ravelobensis*, as a model for a nocturnal, solitary foraging mammal with a dispersed social system. By means of radiotelemetry and bioacoustics we studied the olfactory and vocal behaviour during nocturnal dispersal and reunion of five sleeping groups.

All groups used 3–17 sleeping sites exclusively, suggesting a sleeping site-related territoriality and competition for them. The occurrence of olfactory and vocal behaviour showed an asymmetrical temporal distribution. Whereas marking behaviour was observed exclusively during dispersal, a particular call type, the trill, was used by all groups during reunions. Interestingly, these trills carried group-specific signatures.

Our findings provide the first empirical evidence for nocturnal primates in a natural environment that olfactory signals represent an important mechanism to regulate the distribution of different groups in space, whereas acoustic signals control intra-group cohesion and coordination.

Keywords Primate · Communication · Sociality · Spacing · Cohesion

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Introduction

How members of dispersed social groups regulate their distribution in time and space and how they coordinate group movement and maintain group cohesiveness are fundamental questions in socio-ecology (e.g. Boinski and Garber 2000; Couzin and Krause 2003; de Waal and Tyack 2003). Anthropoid primates, with the exception of the orang-utan, as well as diurnal lemurs share a common organisation pattern, i.e. permanent social groups in which adult individuals live constantly together and interact in foraging, predator detection and defence, offspring rearing or defence of resources (e.g. van Schaik and van Hooff 1983; Wrangham 1987; Janson 2000; Kappeler and van Schaik 2002). The individuals use rich repertoires of visual, auditory, tactile and olfactory signals for social communication (Zimmermann 1992; Hauser 1996; Fleagle et al. 1999). In contrast, the social structure of the nocturnal Malagasy lemurs is highly diverse. Adults of either sex may sleep and forage solitarily and come together primarily for mating, e.g. in the aye-aye (Sterling and Richard 1995). Alternatively, one male and one female of solitary foraging species may form a dispersed pair which sleeps permanently together such as in fat-tailed dwarf (Fietz 1999; Müller 1999), fork-marked (Müller and Thalmann 2002; Schülke and Kappeler 2003) or sportive lemurs (Rasoloharijaona et al. 2003; Zinner et al. 2003). In other species (e.g. mouse lemurs) several individuals form dispersed groups in which animals forage alone but reunite in fairly permanent groups to sleep (Barre et al. 1988; Radespiel 2000; Weidt et al. 2004). Finally, there exist nocturnal lemurs living in permanent pairs which forage and sleep together, for example woolly lemurs (Harcourt 1991). This high adaptive diversity with regard to social structure (Müller and Thalmann 2000; Kappeler and van Schaik 2002) renders nocturnal Malagasy lemurs an ideal model to understand the evolution of communication signals for inter-group spacing and group coordination in primates. Yet, empirical studies addressing this question in nocturnal solitary foraging lemurs are totally lacking.

The golden brown mouse lemur (*Microcebus ravelobensis*) represents an excellent model to investigate inter- and intra-group communication of nocturnal primates. Discovered in 1994 in the National Park Ankarafantsika in northwest Madagascar (Zimmermann et al. 1998), this primate lives in dry deciduous forest, partly sympatric with its sibling species, the grey mouse lemur (*Microcebus murinus*). Both species weigh about 60 g, are omnivorous and show similar feeding habits (Radespiel et al. unpublished), but differ in morphology (Schmelting et al. 2000), genetics (Pastorini et al. 2001) and acoustic communication (Zietemann 2001; Braune et al. 2001). The social organisation of the golden brown mouse lemur was described as a dispersed multimale/multifemale system with a promiscuous mating pattern (Weidt et al. 2004). Individuals usually forage alone at night, but establish long-term, mixed sex sleeping groups of about five individuals during the day. Home ranges overlap within and between sexes and for individuals from the same or even from different sleeping groups. Groups occasionally change their sleeping sites, mainly leaf nests or tree holes. Nevertheless, the composition of sleeping groups remains stable over time.

The aim of our study was to investigate spacing and group coordination in a solitary foraging mammal forming individualised long-term sleeping groups, using the golden brown mouse lemur as a model. First, sleeping sites have been described as potentially limited resources for mouse lemurs (Radespiel et al. 1998). We hypothesised that restricted sleeping sites should lead to competition among groups. Therefore we expected direct or indirect competition at the sleeping sites, reflected in the spacing pattern of the groups' sleeping sites. Second, we postulated that mouse lemurs should have evolved communication signals to gather at a common sleeping site. It is known that mouse lemurs show marking behaviours such as urine-marking, anogenital rubbing and mouth-wiping (Schilling 1979; Buesching et al. 1998) and display a high vocal activity (Zimmermann 1995). We expect that communication signals facilitate the reaggregation of the group members dispersed in space, and coordinate the search for a specific sleeping site. Olfactory and/or acoustic communication signals may contribute to these inter- and intra-group processes and were studied during dispersal and reunion of groups. Third, we hypothesised that vocal signals for group reunion carry long-term group-specific signatures which may provide a means for group recognition and discrimination.

Methods

Study site and data sampling

The study was conducted in the Reserve forestière d'Ampijoroa in the Ankarafantsika National Park (16°19′S, 46°48′E), about 110 km south-east of Mahajanga, northwest Madagascar. Data collection took place in the 5.1-ha research area Jardin Botanique B (JBB) in a dry deciduous forest. In JBB, the golden brown mouse lemur occurs without any other congeneric species. We worked in the field from September to October 2000 and from July to October 2001, covering a period before and during the mating season (Randrianambinina et al. 2003; Schmelting et al. 2000). Data on communication signals were collected in both the years, spacing data in 2001.

We studied five sleeping groups of the golden brown mouse lemur, three of them in both the observation periods (Table 1). We equipped 16 animals with a radio collar (TW-4 button cell tags; Biotrack, Wareham, UK). Six animals from three groups carried transmitters in both the years. In addition, we banded three individuals of two groups with a reflective collar in the second year. Each of the five groups consisted of three to six members (one to five collared and up to three non-collared animals). Sleeping site locations of radio-collared individuals were determined telemetrically during daytime once a day using a portable receiver (TR-4 with RA-14K antenna; Telonics, Inc., Impala, AZ). All detected sleeping sites of the radio-collared mouse lemurs were registered on a map. We defined a sleeping group as individual mouse lemurs that repeatedly slept together (cf. Weidt et al. 2004). Additional data concerning sleeping group composition were collected during observations of radio-collared individuals at dusk and dawn. All sleeping sites occupied by identified group members were counted for the respective group.

An overview of identified individuals and sleeping groups and the data obtained from them for analysis is given in Table 1.

Vocal and behavioural data were collected during sleeping group dispersal in the evening and reunion in the morning. In the evenings, we went to the sleeping sites while the mouse lemurs were still inactive and positioned ourselves about 8–12 m in front of the sleeping site for direct observation. Evening observation sessions referred to as dispersals (n=32; min=2, max=11, median=6 sessions per group) ended when all animals of the sleeping group had left the area visible from the observation position. For morning observation sessions referred to as reunions (n=23; min=2, max=8, median=3 sessions per group), we waited for the group at the previous sleeping site of that group at least 1 h before sunrise. These sessions came to an end after sunrise when the sleeping group members had entered the site and became inactive. Median duration of dispersal and reunion was determined as the time span between the first and the last animal leaving, respectively entering the sleeping site. In each session, we recorded the presence or absence of marking and vocal behaviour using all occurrence-sampling. The vocal behaviour was attributed post-hoc to six different contexts.

For analysis, we counted the number of dispersals and reunions in which the respective behaviour occurred, as well as the number of sleeping groups involved. The number of absolute frequencies of marking and vocal behaviour during dispersal and reunion was compared using the chi-square test. Small sample sizes were adjusted by the Yates method (Zöfel 1992).

Table 1 Representation of studied groups in the data sample[a]

Group	Year 2000[b] Study animal	Collar	comm. signals	group-sp. trill sign.	Year 2001 Study animal	Collar	Spacing (days of ss determin.)	comm. signals	group-sp. trill sign.
1	M 16-99	tr	Yes	Yes				Yes	Yes
	M 02-00	tr							
	F 11-98	tr			F 11-98	tr	41		
	F 09-00	tr			F 09-00	tr			
	F 11-00	tr			F 11-00	tr			
					Non-collared 1.1				
					Non-collared 1.2				
2	F 02-99	tr	Yes	Yes				Yes	Yes
	F 08-00	tr			F 08-00	tr	7		
	F 20-00	tr			F 20-00	tr			
					Non-collared 2.1				
					Non-collared 2.2				
					Non-collared 2.3				
3	M 06-00	tr	Yes	Yes				Yes	Yes
	M 12-00	tr							
	F 24-97	tr			F 24-97	tr	54		
					F 02-01	tr			
					F 15-01	tr			
					F 28-00	ref			
					F 22-01	ref			
					Non-collared 3.1				
4			–	–	F 36-98	tr	56	Yes	Yes
					M 34-00	tr			
					M 09-01	ref			
					Non-collared 4.1				
5			–	–	F 43-00	tr	15	Yes	No
					Non-collared 5.1				
					Non-collared 6.1				

[a]comm. signals: communication signals, group-sp. trill sign.: group-specific trill signatures, ss: sleeping site, F: female, M: male, tr: transmitter, ref: reflective collar

[b]These groups were also part of the study Weidt et al. 2004

Marking behaviour

We distinguished two types of marking behaviours (Schilling 1979; Glatson 1983): urine washing and mouth-wiping. In urine washing, urine is deposited on the hands and then rubbed along the feet. Afterwards, urine marks are placed by running over the substrate. During mouth-wiping, the corner of the mouth, the face and sometimes the head are rubbed along a branch.

Sound recording and analysis

The vocal repertoire of the golden brown mouse lemur extends into the ultrasonic range (Braune et al. 2001; Zietemann 2001). Consequently, a special device for ultrasound recording was necessary. We connected the high-frequency output of a bat detector (U30, Ultrasound Advice) via a filter/control unit (Pettersson) to a high-speed A/D-card (DAS 16/330, Computerboards, Inc.) in a laptop (Compaq Armada) equipped with the recording software BatSoundPro 3.0. The filter/control unit allowed us to 'start' and 'stop' the recordings which were made with a sampling frequency of 200 kHz (16 bit, mono). The use of a circular buffer function made it possible to record the last 10 or 15 s before the recording was stopped. All recorded vocalisations were analysed using BatSoundPro 3.0 (FFT size: 512; Hanning window).

The calls were classified in three categories, i.e. trill, wide-band zip and whistle/tsak (Fig. 1), according to Zimmermann (1995) and Zietemann (2001) by visual inspection of the sonagrams. Between these categories there were no transitions.

Trills were subjected to a more detailed analysis. We analysed 53 trills produced by the three sleeping groups in the year 2000, and 81 trills from these and one additional group in the year 2001. Trills of the fifth sleeping group (group 5) were visually inspected but not of sufficient quality for a quantitative analysis, for example due to background noise, overlapping calls or echo clutter. For

each group, calls from at least two individuals were considered by including non-overlapping trills from overlapping trill series of two different individuals. We measured 22 acoustic parameters for each trill (Table 2): temporal parameters were determined using the waveforms, frequency parameters from the power spectra (BatSoundPro 3.0).

The trills of the four 2001-groups formed the basis for a discriminant function analysis. The 22 acoustic parameters of the 81 trills were tested for correlation (Spearman-Rank-Correlation; Statistica 5.0, StatSoft, Inc.). From a pair of parameters with $r_s > 0.75$, only one was selected for the discriminant function analysis. Parameter pairs with $r_s < 0.75$ were defined as sufficiently non-related (SPSS 11.0, SPSS, Inc.). This method yielded 11 acoustic variables for our analysis (indicated in Table 2) for which medians were calculated. We used the stepwise forward method (statistic: Wilk's-λ) with the criteria $F_{\text{to enter}} = 3.84$ and $F_{\text{to remove}} = 2.71$ and a tolerance level of ≤ 0.01 to calculate the discriminant function model.

The computed discriminant functions were used to classify cases with regard to their group membership. First, the 81 cases of the year 2001 were cross-validated by the "leave-one-out" method, where each case in the analysis was classified by the functions derived from all cases other than that case; for this classification a priori probabilities were dependent on group sizes (SPSS 11.0, SPSS, Inc.). Second, we assumed that groups containing identical individuals in 2000 and 2001 represent the same group. To test whether group signatures of trills remain constant over the years, all cases of the year 2000 were classified as new cases. Here, it was assumed that a case was equally likely to be a member of any group, so a priori probabilities were equal for each group.
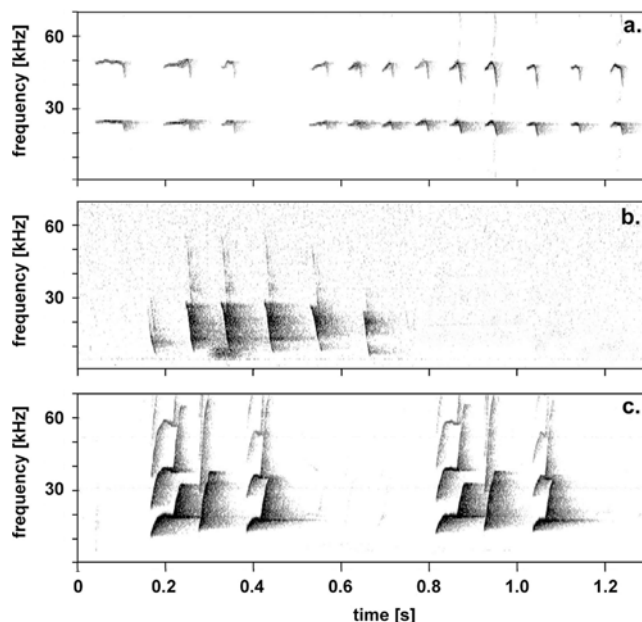
Table 2 Acoustic parameters of trills[a]

Acoustic parameter		Description
Total call		
el		Number of elements per call
f_0 start 1	(kHz))[a]	Start frequency of the fundamental of element 1
f_0 end	(kHz))[a]	End frequency of the fundamental
f_0 min	(kHz)	Minimum frequency of the fundamental
f_0 max	(kHz)	Maximum frequency of the fundamental
band call	(kHz)	Bandwidth of call: f_0 max $- f_0$ min
call dur	(ms)[a]	Call duration
dur el	(ms)	Duration per element: call dur / el
dur min	(ms)	Duration of call from onset to f_0 min
dur max	(ms)	Duration of call from onset to f_0 max
pos f_0 min	(%)[a]	Relative temporal position of minimum: 100/call dur × dur min
pos f_0 max	(%)[a]	Relative temporal position of maximum: 100/call dur × dur max
Elements of the call		
f_0 start 2	(kHz)	f_0 start of element 2
f_0 end 1	(kHz)[a]	f_0 end of element 1
f_0 end 2	(kHz)[a]	f_0 end of element 2
band 1	(kHz)[a]	Bandwidth of element 1: f_0 max of element 1 $- f_0$ min of element 1
band 2	(kHz)[a]	Bandwidth of element 2: f_0 max of element 2 $- f_0$ min of element 2
cf_0 peak 1	(kHz)	Peak frequency of constant f_0-component in element 1
turn 1	(ms)	Onset of second upward component in element 1
dur 1	(ms)[a]	Duration of element 1
dur 2	(ms)	Duration of element 2
int 1_2	(ms)[a]	Interval between onset of element 1 and onset of element 2

[a]Variable which remained after the Spearman-Rank-Correlation for the discriminant function analysis

The tests on number of sessions as well as the discriminant function analysis were based on pooled data for every group because we could not always determine the identity of a marking or calling group member. Therefore we cannot discard the possibility that some individuals, e.g. age-sex groups may have attributed more to the results than others (see Bart et al. 1998).

Fig. 1 Spectrograms (FFT size 512, Hanning window) of: **a.** whistles which turn into tsaks, **b.** wide-band zips and **c.** two trills consisting of three elements each

Results

Spacing

Sleeping groups used between 3 and 17 sleeping sites in 2001. The groups changed their sleeping site every 2–9 days (median=three days). We found the sleeping groups in 98%
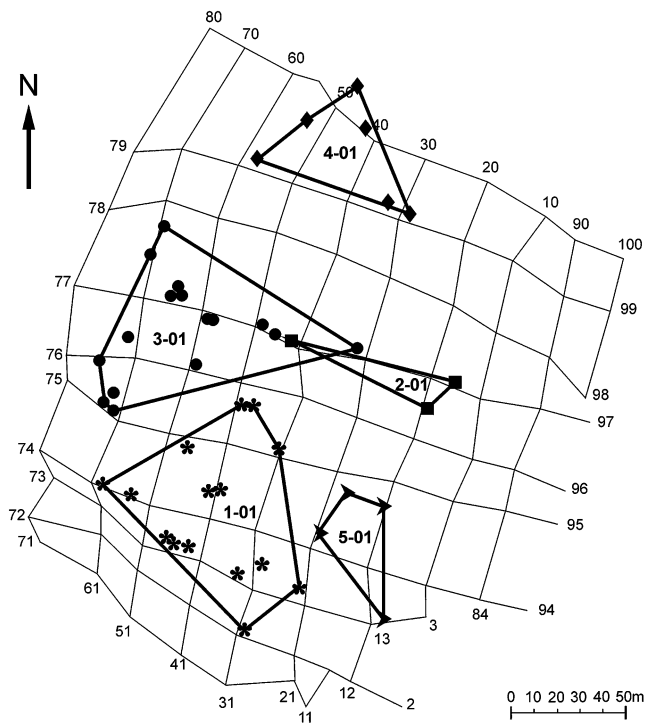
Fig. 2 Distribution of sleeping sites of the five groups in 2001. At the study site JBB a grid system was established. One hundred percent minimum convex polygons are indicated by bold lines

on average of all sleeping site localisations during daytime (cf. Table 1). Sleeping sites were occupied exclusively, i.e. there was no case in which a group slept at a sleeping site of another group (Fig. 2). Due to predation or transmitter problems, we lost several study animals, and in two cases (groups 1 and 2) the whole sleeping group after 41 and 7 days, respectively.

Behaviour during dispersal and reunion

During dispersal the group members left the vicinity of the sleeping site one after another and in the majority of cases they disappeared in different directions (median duration=3 min, $n_{sessions}$=32). During reunion the individuals of a sleeping group arrived at the site in two different ways: they came one by one or as a whole group (median duration=4 min, $n_{sessions}$=16). In the latter case, we could sometimes observe that group members met at a place near the sleeping site and then moved together towards it. Several times, groups came to the previous sleeping site but then decided to change to another. During dispersal and reunion, we recorded distinct communication signals.

Marking behaviour

The mouse lemurs used olfactory signals significantly more often during dispersal (31% of sessions, $n_{sessions}$=32) than during reunion (0% of sessions, $n_{sessions}$=23; χ^2=6.494,

$p<0.05$). No individual showed marking behaviour during reunions, but three individuals of the five groups displayed urine washing (ten times, three groups) or mouth-wiping (four times, two groups) near sleeping sites on 30% of observed dispersals. This olfactory behaviour occurred before and during the mating season.

Vocal behaviour

Vocal behaviour was produced by subjects during both dispersals and reunions. The vocal activity at reunions in the mornings, where calls were recorded in 96% of the sessions ($n_{sessions}$=23), was significantly higher than during dispersal in the evenings, where vocalisations were recorded in only 38% of the sessions ($n_{sessions}$=32; χ^2=16.788, $p<0.001$). The three call categories could occur during a given session. Whistles/tsaks were recorded in about 30% of the observation sessions, but were equally likely produced during dispersals and reunions (χ^2=0.000, $p>0.05$). In contrast, there were prominent differences in the occurrence of wide-band zips (χ^2=5.248, $p<0.05$) and of trills (χ^2=39.928, $p<0.001$) between dispersal and reunion. Zips were only produced during reunions and only in conjunction with trills. They were found in three groups in about 20% of the observation sessions. Trills were found in all five groups and were observed during all reunions besides one. In the remaining case, the whole group entered the sleeping site later in time than on other days without giving any calls. During dispersal, trills were only recorded from male strangers (i.e. males not belonging to the observed group) approaching a sleeping site in the mating season, not from members of the observed sleeping groups.

Context of acoustic signals

The behavioural context in which whistles/tsaks and wideband zips occurred was not clear and is therefore not considered in this analysis. Trills occurred in one specific context during dispersal, and in five during reunion.

During dispersal, trills were uttered in only 2 of 32 sessions by male strangers while inspecting the sleeping site of the observed group. In one session, the caller passed the site quickly while the group members were still at the sleeping site, watching him. In the second session, trills occurred while the group was leaving the sleeping site. We observed chasing and fighting as well as other vocalisations in addition to trills.

In contrast, during reunion, trills occurred in 22 of 23 sessions. We excluded one session from this analysis because the situation was complicated by the presence of a stranger. For trills uttered during the remaining 21 reunions in which only the group members were in the vicinity of the sleeping site, we classified five different contexts, namely 'vocal response' (trills were responded to

Table 3 Selected acoustic variables from 81 trills of four sleeping groups (for parameter definitions see Table 2). Medians are presented for each group and the whole data set

Acoustic parameter	Group 1 (n=12)	Group 2 (n=19)	Group 3 (n=37)	Group 4 (n=13)	All groups (n=81)
call dur (ms)	156.5	260.0	231.0	315.0	266.0
pos f_0 min (%)	74.3	77.0	79.2	0	73.0
pos f_0 max (%)	53.3	29.5	50.6	59.4	52.8
f_0 start (kHz)	14.8	13.3	21.1	14.0	14.1
f_0 end (kHz)	33.0	36.1	38.3	34.8	35.4
f_0 end 1 (kHz)	32.7	37.0	35.9	31.9	33.5
f_0 end 2 (kHz)	34.1	37.3	38.5	35.9	36.9
band 1 (kHz)	18.0	24.1	15.5	18.6	19.3
band 2 (kHz)	20.4	22.3	18.8	17.9	19.3
dur 1 (ms)	58.5	69.0	48.0	74.0	69.0
int 1_2 (ms)	109.5	107.0	90.0	108.0	106.0

by uttering trills and approaching the caller, $n_{sessions}$=1), 'phonotactic approach' (trills caused an approach to the caller, $n_{sessions}$=5), 'phonotactic aggregation' (trills resulted in an aggregation of group members, the caller could not be identified, $n_{sessions}$=6), 'group movement' (trills were recorded while the whole group or a part of it was moving towards the sleeping site, the caller could not be identified, $n_{sessions}$=15) and 'no responding animal present' (single individuals called but no other group members were visible, $n_{sessions}$=3).

Trill structure

Trills consisted of two to six harmonically structured syllables or elements (Fig. 1). In general, elements were upward frequency modulated. The initial and final element started with a steep upward frequency modulation followed by a nearly constant frequency component and terminated with a second steep frequency modulated component. In the centre elements, the nearly constant frequency component was often missing. Sometimes the elements ended with a constant frequency or downward frequency modulated hook. The duration of trills was between 120 and 400 ms. Minimum frequencies of the fundamental ranged from 9 to 18 kHz, maximum frequencies of the fundamental from 28 to 50 kHz. For the 11 acoustic parameters used for a detailed analysis (see 'group-specific signatures of trills') we present medians in Table 3.

Group specific signatures of trills

The stepwise forward discriminant function analysis used 6 of the 11 variables for model calculation, namely start frequency, call duration, bandwidth of element 1, duration of element 1, relative position of minimum frequency and end frequency. Three functions were computed explaining a significant part of the acoustic variability between the four groups (Wilks' λ=0.037; $F_{(18,204)}$=24.9; $p<0.001$; Table 4).

In the year 2001, 92.6% of cross-validated cases were classified correctly and 73.6% of the trills from the year 2000 were allocated to their respective group of 2001 (Table 5). A chi-square test revealed that this distribution is significantly different from chance in each group (group 1: χ^2=46.67, $p<0.001$; group 2: χ^2=9.0, $p<0.029$; group 3: χ^2=19.89, $p<0.001$). Thus, trills provided sufficient information to discriminate between neighbouring groups in our study area.

Discussion

Our study revealed an exclusive use of several sleeping sites by the observed sleeping groups of the golden brown mouse lemur. Communication signals used by group members during dispersal and reunion differed markedly. Marking behaviour occurred exclusively in the evenings during dispersal. In vocal behaviour, the distribution of trills showed

Table 4 Acoustic variables which were entered in the discriminant function analysis[a]

Variable	Entered at step	Wilks-Lambda	F to remove	Tolerance	Function 1 (4.98; 66.4)	Function 2 (1.97; 26.5)	Function 3 (0.53; 7.1)
F_0 start	1	0.098	38.761	0.186	0.452	0.604*	−0.385
call dur	2	0.068	19.260	0.793	0.257	−0.654*	0.605
band 1	3	0.051	9.049	0.561	−0.320	−0.005	0.850*
dur 1	4	0.059	13.677	0.299	−0.082	−0.617*	0.291
pos min	5	0.046	5.579	0.667	−0.0 27	0.266*	0.070
f_0 end	6	0.045	4.806	0.867	0.165	0.287	0.344*

[a]The statistics are given for every variable at step 6 of the analysis. The structure matrix contains within-group correlations of each predictor variable with the canonical function. For each variable, an asterisk marks its largest absolute correlation with one of the canonical functions. Eigenvalues and percentage of variance are given for each function

Table 5 Classification results for trills on the basis of the three calculated functions which discriminate between the four sleeping groups of the year 2001. These 81 cases (groups 1-01–4-01) were cross-validated (A). Trills of the year 2000 (groups 1-00–3-00) were classified as new cases (B)[a]

	Correct (%)	In group 1-01	2-01	3-01	4-01
(A) Cross validation (2001)	92.6				
Group 1-01 (n=12)	83.3	10	1	1	0
Group 2-01 (n=19)	89.5	0	17	2	0
Group 3-01 (n=37)	100	0	0	37	0
Group 4-01 (n=13)	84.6	0	1	1	11
(B) New original (2000)	73.6				
Group 1-00 (n=36)	72.2	26	2	8	0
Group 2-00 (n=8)	62.5	3	5	0	0
Group 3-00 (n=9)	88.9	0	0	8	1

[a] '*n*': number of trills included in the analysis per group

a reversed asymmetry: they were recorded regularly during reunion in the morning, whereas, during dispersal, we recorded them only twice in the mating season and only when strangers were present. The trills of the different groups carried specific signatures.

Spacing

Safe sleeping sites protect individuals and groups against predators and adverse climatic conditions. If those sites represent limited resources like the tree holes or nests used by mouse lemurs (Radespiel et al. 1998, 2003), competition for them should be expected. Indeed, the exclusive sleeping site usage in the golden brown mouse lemur may reflect an indirect competition. A similar pattern is characteristic for a variety of animals which sleep in nests or tree holes, for example other nocturnal lemurs such as sportive lemurs (Rasoloharijaona et al. 2003), fork-crowned lemurs (Charles-Dominique and Petter 1980), fat-tailed dwarf lemurs (Müller 1999), and other mammals such as bats (Kerth et al. 2002).

The ownership of several safe sleeping sites may be indispensable for survival and reproductive success. The use of several sleeping sites scattered in space, however, raises three problems for a solitary ranging but communal nesting species: how to advertise the ownership of a given site, how to relocate it, and how to gather at a particular site and a distinct time on each day.

Marking behaviour

Marking behaviour at sleeping sites, predominantly urine-washing, occurred during dispersal but never during reunion. A similar pattern was found in female sleeping groups of the grey mouse lemur (Glatson 1983; Peters 1999).

Marks could on the one hand facilitate the relocation of the animals' own sleeping sites (e.g. Seitz 1969) and could on the other hand serve to establish the group ownership of a sleeping site (e.g. Wyatt 2003) in order to reduce conflict between groups for a limited resource (e.g. Charles-Dominique 1977; Mertl-Millhollen 1988; Swaisgood et al. 2000). These relocation- and conflict avoidance hypotheses are supported by our data: if marking

serves to relocate the sleeping sites there is no need for marking after relocation. Likewise, if marks indicate ownership and act as a signal to monopolise sites and to deter members of other groups, marks should be refreshed at the beginning of the active period in the evenings.

Vocal behaviour

Olfactory signals are not sufficient to attract and to guide group members at a particular time to a specific sleeping site. As groups change their sleeping sites from time to time (see this study and Weidt et al. 2004) the group members need signals which are not only attributable to the own group but also are indicators for a specific location at a particular moment. In dense forest, at night, acoustic signals are adequate communication signals to achieve these tasks. Observations in African galagos and pottos summarised in Bearder et al. (2003) suggest that vocalisations are important for group cohesion. Indeed, we found a specific call type, the trill, which occurred regularly during the reunions of sleeping groups. The trill may serve different functions: mate attraction/mate defence (Buesching et al. 1998; Zimmermann et al. 2000), resource defence and group coordination. According to the mate attraction- / mate defence-hypothesis, males and females of the golden brown mouse lemur should use trills during the mating season for courtship and/or to deter competitors. Similar vocal behaviours in the mating context are known for the grey mouse lemur (Zimmermann and Lerch 1993; Hafen 1998) and the coquerel's dwarf lemur (Stanger 1995) as well as for other nocturnal strepsirrhines: bushbabies (Bearder and Doyle 1974; Zimmermann 1985a), slender loris (Radhakrishna and Singh 2002), slow loris (Zimmermann 1985b) and pottos (Charles-Dominique 1977). Moreover, trills used in the reproductive context were found in captive golden brown mouse lemurs (Polenz 2000; Zietemann 2001). Thus, the mate attraction- / mate defence-hypothesis may account for the trills recorded during dispersals. In the two dispersal cases where we heard trills, male strangers were in the area and presumably searching for oestrous females, and in one of these cases fights broke out.

However, the mate attraction- / mate defence-hypothesis is not sufficient to explain the occurrence of all trills: during reunions we recorded trills even 1 month before the beginning of the mating season (for reproduction cycle see

Randrianambinina et al. 2003). In addition, this hypothesis cannot explain the temporal asymmetry in the occurrence of trills in our study, in which trills were uttered mainly during reunions.

Both, the resource defence- and the group coordination hypothesis are supported by the above temporal asymmetry. For resource defence, however, the group members are expected to use trills regularly at the resource, i.e. the sleeping site. In our study, trills occurred only occasionally at the sleeping site, whereas, in most cases, the individuals uttered trills before they reached the respective site: trills were predominantly uttered while members of a group aggregated in the vicinity of the sleeping site or while the whole group was moving towards the site. This renders it unlikely that the main function of trills is resource defence.

Three lines of evidence support the group coordination hypothesis. First, during reunions, trills of a group member never attracted collared members of other groups. Similarly, Weidt et al. (2004) which had fully collared groups never found strangers joining a sleeping group. Second, during four reunions, group members already present at the sleeping site left it to meet arriving individuals. Afterwards they returned together to the sleeping site. In this situation, trills were uttered. Finally, members of a group uttered trills during group movement towards the sleeping sites.

Group-specific acoustic signatures

A prerequisite for vocalisations regulating group coordination is their inter-group acoustic distinctiveness. Group differences may be based on individual differences or on group signatures. Individual call signatures have been reported for a number of primate species (e.g. Marler and Hobbett 1975; Zimmermann and Lerch 1993; Hammerschmidt and Todt 1995) and may have a perceptual relevance for conspecifics (e.g. Snowdon and Cleveland 1980; Cheney and Seyfarth 1982; Rendall et al. 1996). In our study, we could not always attribute the trills to the respective caller due to observational constraints at night. Overlapping series of trills from different individuals were found in all sleeping groups indicating that at least two individuals of the same group were calling and contributed to our sample. Thus, the characteristic differences in the trills between groups represent group signatures rather than those of single individuals. The signatures of the groups tested both in 2000 and 2001 showed a high degree of similarity. Group-specific signatures have been found in a variety of birds (Nowicki 1989; Hopp et al. 2001) and mammals (e.g. dolphins: Watwood et al. 2004; bats: Boughman and Wilkinson 1998; Dörrie et al. 2001).

Our study is the first account of group-specific signatures in group coordination calls of a nocturnal primate. The signatures may be explained by two different factors, inheritance (Winter et al. 1973; Scherrer and Wilkinson 1993), or acoustic convergence, especially within non-kin groups (e.g. Mundinger 1982; Zimmermann and Hafen 2001; Boughman 1997). Generally, the vocal system of

anthropoid non-human primates is considered to be relatively unaffected by learning (e.g. Seyfarth and Cheney 1997). However, several studies suggest that the social environment may influence social call structure (e.g. Egnor and Hauser 2004) .

Conclusion

Our study presents the first context-related and quantitative evidence for mechanisms regulating inter-group spacing and intra-group cohesion in a nocturnal primate species. Most interestingly, we revealed that a call with group-specific signatures, the trill, is used during group coordination. So far, group coordination calls have only been shown for a number of diurnal permanently group-living primates (e.g. Boinski and Garber 2000) but not for nocturnal primates. Moreover, we have shown in the present study that trills of comparable structure may be used for mate attraction and/or mate defence. This suggests that group coordination calls might originate from mate attraction and/or mate defence calls, thus providing insight into the mechanisms driving the evolution of vocal communication.

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