Acoustic variability and its biological significance in nocturnal lemurs

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Contents

1 Abstract

The aim of this thesis was to examine the acoustic variability and its biological significance in nocturnal lemurs from an evolutionary point of view. The grey (*Microcebus murinus*) and the golden brown (*Microcebus ravelobensis*) mouse lemur and the Milne Edwards' sportive lemur (*Lepilemur edwardsi*) from the same ecological community were used as model species in this comparative study. These species are nocturnal, arboreal primates living in the dry deciduous forests of north western Madagascar. Mouse as well as sportive lemurs represent ancestral forms in primate evolution due to several morphological and behavioural features. Individuals of both genera are solitary ranging but form stable sleeping groups or pairs, respectively. Mouse lemurs live in a multi-male / multi-female system with a promiscuous mating pattern characterised by scramble competition among males. In contrast, Milne Edwards' sportive lemurs live in stable pairs sharing an exclusive territory. Both genera show a high vocal activity offering the potential for inter- and intra-specific communication. For this thesis, three bioacoustic studies were conducted. Therefore, several factors, which may have an influence on call functions and their biological significance within and between species have been analysed. In the first and second study the intra-specific call variability of golden brown mouse lemurs and Milne Edwards' sportive lemurs was analysed by observing mouse lemur sleeping groups and sportive lemur pairs during dispersal and reunion. Results revealed individual signatures in Milne Edwards' sportive lemur loud calls and group-specific signatures in golden brown mouse lemur gathering calls providing the potential for individual- or group-specific recognition and discrimination. An inter-specific comparison of the results suggested that call variability differences were due to different functions in the light of their social systems. This issue was further discussed with respect to general aspects of primate loud call evolution. In the third study the inter-specific call variability of mouse lemur calls was tested via playback experiments with grey mouse lemurs. These showed varying levels of significance for the different degrees of species-specificity in mouse lemur calls. For advertisement calls of mouse lemurs an effect of sympatry and allopatry could be revealed and was discussed in the light of speciation processes in these cryptic species. The presented thesis showed that the study of acoustic communication on species representing ancestral forms within the primate evolution – such as nocturnal lemurs – allows an interesting insight into a better understanding of speciation processes and the evolution of complex social organisations.

Key words: *Microcebus*, *Lepilemur*, acoustic communication

2 Zusammenfassung

Das Ziel dieser Arbeit war die Untersuchung der akustischen Variabilität und ihrer biologischen Bedeutung bei nachtaktiven Lemuren aus evolutionsbiologischer Sicht. Als Modellarten wurden in dieser vergleichenden Studie der graue (*Microcebus murinus*) und der goldbraune (*Microcebus ravelobensis*) Mausmaki und der Edwards’ Wieselmaki (*Lepilemur edwardsi*) aus derselben ökologischen Gemeinschaft verwendet. Diese Arten sind nachtaktive, baumbewohnende Primaten, die in den Trockenwäldern Nordwest-Madagaskars leben. Sowohl Mausmakis als auch Wieselmakis repräsentieren aufgrund mehrerer morphologischer und verhaltensbiologischer Merkmale Urformen in der Primatenevolution. Die Individuen beider Gattungen verbringen ihre Aktivitätszeit solitär, bilden aber stabile Schlafgruppen, bzw. –paare. Mausmakis leben in einem *multi-male / multi-female*-System mit einem promiskuitiven Paarungssystem welches durch *scramble competition* zwischen den Männchen gekennzeichnet ist. Im Gegenteil dazu leben Wieselmakis in stabilen Paaren, die abgegrenzte Territorien bewohnen. Beide Gattungen zeigen ein ausgeprägtes vokales Verhalten, wodurch die Möglichkeit zur zwischen- und innerartlichen Kommunikation besteht. Für diese Arbeit wurden drei bioakustische Studien durchgeführt. Dazu wurden verschiedene Faktoren untersucht, die Ruffunktionen und ihre biologische Bedeutung innerhalb und zwischen Arten beeinflussen können. In der ersten und zweiten Studie wurde die innerartliche Rufvariabilität bei goldbraunen Mausmakis und Edwards’ Wieselmakis analysiert. Dazu wurden die Schlafgruppen der Mausmakis und die Wieselmaki-Paare während ihres Zerstreuens und Zusammenfindens beobachtet. Die Ergebnisse zeigten individuelle Signaturen der Edwards’ Wieselmaki *long calls* und gruppen-spezifische Signaturen in den *gathering calls* der goldbraunen Mausmakis, die somit zur individuellen bzw. gruppen-spezifischen Erkennung und Unterscheidung dienen können. Ein Vergleich zwischen den beiden Arten deutete darauf hin, dass die Unterschiede in den Rufvariabilitäten dieser beiden Arten auf verschiedene Ruffunktionen angesichts ihrer Sozialsysteme verstanden werden können. Dieses Ergebnis wurde des Weiteren im Hinblick auf generelle Aspekte der *loud call*-Evolution bei Primaten diskutiert. In der dritten Studie wurde die Rufvariabilität bei verschiedenen Mausmaki-Arten mittels Playback-Experimenten an grauen Mausmakis getestet. Hierbei ergab sich ein unterschiedlicher Bedeutungsgrad zweier Mausmaki-Ruftypen, die einen unterschiedlichen strukturellen Grad an Artspezifität zeigten. Für die Anzeigelaute der Mausmakis konnte ein Effekt von Sympatrie und Allopatrie ermittelt werden, welcher in Hinblick auf Artbildungsprozesse dieser kryptischen Arten diskutiert wurde. Die vorliegende Arbeit zeigt, dass die Erforschung der akustischen Kommunikation bei Arten, welche – wie die Lemuren – nahe am Anfang der Primatenevolution stehen, interessante Einblicke für ein besseres Verständnis von Artbildungsprozesssen und die Evolution komplexer Sozialstrukturen ermöglichen.

Schlagwörter: *Microcebus*, *Lepilemur*, akustische Kommunikation

3 General introduction

3.1 Animal communication

Variability in the communication system of animals has evolved on the intra- as well as on the inter-species level. In any case, information is conveyed from a sender by a specific channel to a receiver influencing his physiology or behaviour (cf. Endler 1993; Bradbury and Vehrencamp 2000).

Animals can rely on a variety of sensory modalities for example the tactile, olfactory, visual and acoustic channel. The usefulness of certain modalities for purposes of communication depends on several external factors as for example habitat characteristics (e.g. Morton 1975, Wiley and Richards 1978) the organisms' activity rhythm or predator pressures (cf. Marler 1955). Furthermore, a special sensory modality may be more useful for specific concerns than others: for example, important current information should be transmitted by a fast channel, whereas, long-lasting signals may have another priority. Moreover, the signals' applicability for short and long distance information transfer decides on the successful implementation of a communication channel.

Tactile signals play an important role in short distance communication. On the one hand they are used during tactile interactions involving positive, aggregative tendencies such as grooming or parent – offspring interactions (cf. Marler 1967; Bradbury and Vehrencamp 1998). On the other hand they are also implemented during negative, dispersive interactions such as fights and formalised gestures of domination.

Olfactory signals can be useful for short and long distance communication. Scent marks persist during the absence of the signalling animal and do not require the precise position of the signaller at any moment (Marler 1965). These signals may for example serve for inter-individual and inter-group spacing (cf. Sussman 1992) or oestrus advertisement (Brown 1979; Taylor and Dewsbury 1990). Furthermore, they may support the orientation towards or away from the sender, or, facilitate the orientation in the animals' home range (e.g. insects: Wilson 1962; primates: Sauer and Sauer 1963; Seitz 1969). On the other hand, olfactory signals are relatively slow and do not enable the advertising of complex information over longer distances at a specific moment of time.

Visual signals provide most the advantages concerning the localisation of the signaller and the high variability of potential channels for an inexpensive information transfer, for example, motion speed and direction, brightness, hue etc. (Endler 1993). On the other hand, successful signalling strongly depends upon ambient light and the absence of barricades; visual signals are not useful unless there is a clear path.

In contrast, acoustic communication is independent of time and place and provides a lot of advantages especially in the case of long distance communication even in vision reduced habitats. Through this directed signal a calling animal may be localised at a particular moment at its current site. For this purpose birds and mammals rely mainly on binaural detection of differences in intensity, phase, and time of acoustic signal (Marler 1967). However, vocalisations underlie several environmental effects such as attenuation and degradation (e.g. Waser and Waser 1977; Wiley and Richards 1982; Brown and Gomez 1992) and should therefore be optimised concerning habitat characteristics and their biological function through natural selection (Morton 1975; Endler 1993; Ryan and Kime 2003). Apart from this, acoustic signals enable a rapid exchange of information even with modifications of signal characteristics when necessary (Marler 1967). Additionally, they can be generated and heard without other activities being disrupted.

As documented in simian primates, vocalisations can encode information about the sender such as its sex, age, individual identity, internal state and behavioural intentions (for reviews see: Snowdon et al. 1982; Todt et al. 1988; Cheney and Seyfarth 1990b; Zimmermann 1992). Furthermore, calls can provide information about the quality of a predator or a food source or about social relationships.

3.2 Acoustic variability on the inter- and intra-species level

Acoustic signals offer a broad range of applications for inter- and intra-specific concerns. First of all, individuals of species living in the same ecological community have to discriminate between conspecifics and heterospecifics primarily regarding successful reproduction. Especially in solitary ranging species or in those where males and females live separated from one another the localisation of an adequate mating partner requires species-specific signals to minimise time and energy loss for searching for a mate (Bradbury & Vehrencamp 1998).

Long distance communication signals such as loud (or long) calls for mate attraction often carry species-specific signatures. These represent valuable tools to facilitate or even allow meetings of mating partners through mate recognition (Marler 1967) because they are independent of time and place. Nevertheless, they give precise information of the senders’ position and may transfer information about the current status, the fitness, or intention of the sender (Hauser 1997; see chapter 3.1).

Inter-specific signal variation is expected to be most important in areas where closely related cryptic species, which look remarkably similar (Mayr 1977; Templeton 1998), occur sympatrically. Here, mating partners do not only have to localise each other, but, they also have to discriminate between conspecifics and heterospecifics. Thus, it was assumed that in areas of sympatry a high selection pressure exists towards production and perception systems of species-specific calls involved in reproduction (e.g. Mayr 1977; Paterson 1985; Templeton 1989; Andersson 1994).

Due to this strong sexual selection pressure, species-specificity in communication systems may evolve faster than in morphological traits (Jones 1997; Yoder et al. 2002). Species-specific signalling systems on the basis of vocalisations may act as premating isolation mechanisms for cryptic species in order to avoid costly hybridisation (Mayr 1977; Paterson 1985; Templeton 1989; Andersson 1994).

It is commonly known that closely related sympatric species have evolved significant structural differences in calls involved in the process of reproduction (e.g. Ryan 1990; Jones 1997). Empirical data on the perception of species-specific calls have been made and the biological relevance of such calls in sympatrically living animals have been raised in several species (e.g. katydids: Gwynne and Morris 1986; crickets: Honda-Sumi 2005; frogs: Höbel and Gerhardt 2003; birds: de Kort and ten Cate 2001). However, such data are lacking for primates so far.

Intra-specific call variation is highly important in gregarious animals. In contrast to solitary living species special advertisement calls for mate attraction may be of secondary interest for these species (Bradbury & Vehrencamp 1998). On the other hand group-living individuals rely on communication cues to keep in contact and to manage intra- and inter-group concerns (cf. Oliveira and Ades 2004). Thus, differences in social systems should require different communication features which can be reflected in their acoustic signals (Marler and Mitani 1988; Masataka and Thierry 1993).

According to this, for example long calls of primates can be used for intra-species communication as territorial defence in territorial species (Mitani 1985b; Masataka and Thierry 1993; Geissmann 1999) or for group cohesion (Robinson 1982; Mitani and Nishida 1993; Norcross and Newman 1993; Janik and Slater 1998; Sugiura 1998) and group retrieving (Lieblich et al. 1980; Waser 1982; Snowdon 1986) in gregarious species.

For these aspects of intra-specific acoustic communication vocalisations have to convey specific messages. Indeed, it was shown in a variety of species that these traits can be encoded acoustically as for example in kinship- (e.g. macaques: Rendall et al. 1996), group- (bats: Boughman 1997), sex- (e.g. gibbons: Haimoff 1986; Geissmann 2002) or individual signatures (primates: e.g. Macedonia 1986; Zimmermann and Lerch 1993; Riede 1997; Teixidor and Byrne 1999). The acoustic characteristics of an individual's call may be inherited or learned as was shown for example in the case of bats, seals, dolphins and primates (cf. Janik and Slater 1997).

For this thesis I studied the variability of animal acoustic communication using nocturnal lemurs as models. This group of ancestral primates, belonging to our closest biological relatives – the non-human primates – have a variety of advantages.

3.3 Malagasy lemurs

Malagasy lemurs represent a monophyletic infraorder (Lemuriformes) and are all endemic to Madagascar. They are assumed to have originated from a common ancestor starting from the African mainland (Martin 1995) between 50 and 70 Million years ago (Yoder et al. 1996). Lemurs have undergone an adaptive radiation resulting in 16 extinct and 71 currently known living species and subspecies (status quo: Mittermeier et al. 2006). They represent the most ancestral living primates retaining a suite of ‘primitive’ characteristics as for example the presence of a tapetum lucidum, a rhinarium and special jaw morphology (Geissmann 2003).

The species have evolved several adaptive strategies in physiology with regard to seasonality: they have a reduced resting metabolic rate (RMR) up to 20% below that of the mammalian mass-specific standard (reviewed in Müller 1985; Genoud et al. 1997). Several lemurs undergo seasonal body mass changes through seasonal fattening (some Cheirogaleidae: e.g. Fietz 1998; Schmid 1999; Atsalis 1999), or, they reveal metabolic adaptations in various hormones (*Lemur catta* and *Eulemur fulvus rufus*; Pereira et al. 1999).

Furthermore, certain members of the Cheirogaleidae show daily (*Microcebus*: e.g. Charles-Dominique and Petter 1980; Schmid et al. 2000) or prolonged (*Cheirogaleus medius, C. major*: e.g. Charles-Dominique and Petter 1980*; M. murinus*: Schmidt and Kappeler 1998; Schmid 1999, Schmid 2000) seasonal torpor marked by a reduction in metabolic rate and lowered body temperature representing a unique pattern among primates (cf. Schmid and Stephenson 2003). Additionally, behavioural thermoregulation to conserve energy for selection of advantageous microhabitats, changes in body posture and huddling with conspecifics was reported in several lemur species (Sussman 1974; Tattersall 1982).

Some lemurs have a diurnal life-style including the genus *Propithecus*, the *Lemur catta* and the *Indri indri*. All of them live gregariously in groups of about 3 - 17 animals and form cohesive foraging groups as those commonly found in diurnal simians (Goodman et al. 2003). The cathemeral lemur species (according to Tattersall 1987) like the genus *Eulemur* and *Hapalemur* are group-living with 3 - 10 individuals per group (Goodman et al. 2003).

In contrast, the social systems of nocturnal lemurs are highly diverse (e.g. Müller and Thalmann 2000). First of all, the individuals of a species may live solitarily as 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 as for example the mouse lemurs several individuals form dispersed groups in which animals forage alone but reunite in groups to sleep (Barre et al. 1988; Radespiel 2000; Weidt et al. 2004). Finally, nocturnal lemurs living in permanent pairs exist. These woolly lemurs forage and sleep together (Harcourt 1991).

Malagasy primates reflect a natural experiment of evolution (Ganzhorn and Kappeler 1993). In the case of small primates living in dense habitats such as forests visual communication is limited. Thus, olfactory and particularly acoustic communication have more advantages for long distance communication (e.g. Bearder 1987; Zimmermann 1995a). Therefore, nocturnal lemurs are ideal models for studying the variability in acoustic communication signals. The obtained results are of particular interest for the understanding of primate evolution as they may indicate early socio-communicative adaptations within the primate radiation.

3.4 Model species of nocturnal lemurs

In this thesis I present results concerning the variation of acoustic behaviour and its biological significance on the inter- and intra-specific level by focussing on three nocturnal lemur species belonging to the same nocturnal lemur community: the grey and the golden brown mouse lemur (*Microcebus murinus* and *M. ravelobensis*) and the Milne Edwards' sportive lemur (*Lepilemur edwardsi*).

Mouse lemurs belong to the family Cheirogaleidae and are the smallest primates in the world ranging in weight from 30-90g (Mittermeier et al. 2006). They represent the most abundant group of primates on Madagascar (Garbutt 1999) including fifteen known cryptic species which are difficult to distinguish in body characteristics (Zimmermann et al. 1998; Rasoloarison et al. 2000; Yoder et al. 2000; Kappeler et al. 2005; Olivieri et al. 2006 in review).

Mouse lemurs inhabit the fine branch niche of Malagasy forests (Harcourt and Thornback 1990) with one or two *Microcebus*-species co-occurring in a given habitat. They are omnivorous and use a large variety of food sources dependent on seasonal availability, including fruits, gum, insects, insect secretions, leaves, flowers, nectar, arthropods and small vertebrates (Radespiel et al. 2006; Joly unblished data).

Mouse lemurs are strictly nocturnal and spend the day in sleeping groups of 2-6 individuals, which have overlapping home ranges (Radespiel 2000; Weidt et al. 2004). In the case of the grey mouse lemur genetically related females sleep together and males only occasionally have sleeping partners (Radespiel et al. 1998, Radespiel et al. 2001b) whereas in the case of the golden brown mouse lemur mixed-sexed sleeping groups are formed (Weidt et al. 2004).

Individuals of both species are known to mark frequently (e.g. Glatson 1983; Weidt et al. 2004), but in contrast with a variety of other lemurs they do not exhibit specialised scent glands. Instead they use saliva, faeces or in most cases urine as chemical signals (Schilling 1979, Perret 1995). These marks were assumed to have a function for example in oestrous advertisement (Buesching et al. 1998), maternal behaviour (Perret 1995) and dominance advertising (Doyle 1975; Glatson 1983).

Mouse lemurs vocalise in a frequency range from about 0.5 to about 40 kHz (Zimmermann 1995a; Zietemann 2001) and their hearing sensitivity is best in the range of 10 and 24 kHz (Niaussat and Petter 1980). They show a rich repertoire of different call types including advertisement, alarm / attention and aggressive calls, which are uttered by both sexes in various contexts (Zimmermann 1995a; Polenz 2000; Zietemann 2001). Most call types are tonal and display a harmonic structure. For male mating advertisement calls individual-specific call parameters were documented within a population (Zimmermann and Lerch 1993; Hafen 1998; Polenz 2000). In the case of grey mouse lemurs dialects between different populations have been shown as well (Hafen et al. 1998).

Sportive lemurs belong to the family Lepilemuridae. The genetically identified twenty-four species of this family (Louis et al. 2006; Rabarivola et al. 2006; Craul et al. 2006 submitted) are widely distributed over Madagascar and can be found in almost all forested regions (Mittermeier et al. 1994; Thalmann and Ganzhorn 2003).

Sportive lemurs are cat-sized vertical clingers and leapers occurring in almost all natural evergreen or deciduous forests. Their body mass ranges from between 500g to 1000g and this genus therefore represents, together with woolly lemurs, the smallest predominantly folivorous primates in the world. This is most probably due to their extremely low resting metabolic rates (see above: reduction of RMR; Schmid and Ganzhorn 1996).

All sportive lemur species are strictly nocturnal. They forage solitarily during the night and inhabit well-defined home ranges between 0.3 and 1.2 ha. Most individuals rest together with one to three conspecifics during the day. Past studies concerning their social organisation revealed different results. However, for the moment, it is most likely that at least the Milne Edwards' sportive lemur (*Lepilemur edwardsi*), which is the studied species in this thesis, exhibits a dispersed monogamous pattern (cf. Müller and Thalmann 2000; Rasoloharijaona et al. 2003).

This species lives in stable male-female pairs (including their young offspring) which disperse for foraging but share the same home range exclusively (Rasoloharijaona et al. 2003). Being an exception among the lemurs, Milne Edwards' sportive lemurs have never been observed to mark (Rasoloharijaona et al. 2003). Nonetheless, studies suggest a high vocal activity in these species (Rasoloharijaona and Zimmermann 2000).

3.5 Intra-specific variation in acoustic communication of two species of nocturnal lemurs

As mentioned above, both nocturnal lemur species studied for intra-specific acoustic communication patterns, namely the Milne Edwards' sportive lemur and the golden brown mouse lemur, show similarities and but also obvious differences in their social structure and behaviour. Both are solitary foragers but form stable mixed-sexed pairs or groups, respectively, for their inactive period during the day. In both species sleeping associations use special nesting sites as tree holes or dense vegetation (e.g. Harcourt and Thornback 1990; Rasoloharijaona et al. 2003 for Milne Edwards' sportive lemurs; Weidt et al. 2004) for golden brown mouse lemurs). These sites have been assumed to represent limited resources for mouse lemurs (Radespiel et al. 1998) as well as for sportive lemurs (Rasoloharijaona et al. 2003).

Therefore, in both species competition for these limited sites could be expected. Competitive behaviour could be exhibited by aggressive interactions, or, indirectly, using special communication cues avoiding costly physical contests. Due to the fact that nocturnal prosimians have limited vision compared to diurnal species (Pariente 1979, but see Piep et al. 2003; Bearder et al. 2006) olfactory and acoustic communication signals should be of high importance due to their nocturnal life-style and their dense forest habitat.

With regard to marking behaviour mouse and sportive lemurs showed obvious differences: Unlike the mouse lemurs sportive lemurs showed no marking behaviour whatsoever. But, although they differ in this olfactory behaviour, both groups show a high vocal activity (Martin 1972; Zimmermann 1995a; Rasoloharijaona and Zimmermann 2000) providing a high potential for intra- and inter-group communication.

Another difference between the two studied species is the number of used sleeping sites in the course of time: pairs of sportive lemurs were only found at 1-3 different sites (Rasoloharijaona et al. 2003) whereas the groups of golden-brown mouse lemurs used up to 16 different sleeping sites during six months (Weidt 2001). Unlike the sportive lemurs, which can be relatively sure about the return of their partner to the sleeping site, in golden brown mouse lemurs the re-aggregation of group members at varying sites requires the use of special communication signals.

The variability, specificity and function of loud calling strongly depend on the social system of a species (cf. Wich and Nunn 2002): For example loud calls functioning in mate defence would primarily be uttered by males of a species. Counter-calling of the sexes could imply mate attraction (Waser and Waser 1977; Mitani 1985b). Furthermore, resource defence through loud calls (e.g. Tenaza 1989; Mitani 1990; Wich et al. 2002) could be expected in mating systems characterised by resource defence polygyny, in which males defend resources needed by females (Clutton-Brock 1989; Fashing 2001), or, in monogamous systems, if males defend resources used by females to invest in their offspring.

Therefore, the study of the occurrence and function of acoustic signals at sleeping sites during dispersal and reunion of groups is one aspect of this thesis so as to investigate the function of loud calling in the two genera of nocturnal lemurs differing in their social systems.

3.6 Inter-specific variation and species-specificity in acoustic communication of mouse lemurs

According to Andersson (1994), in a system of scramble competition the early search and localisation of mates is a crucial factor. As already mentioned mouse lemurs live in a dispersed social system and males are assumed to compete for mates by scramble competition (Radespiel et al. 2001a; Eberle and Kappeler 2004b).

During the mating season the males’ testis size rapidly increases (Schmelting et al. 2000) and they actively search for oestrous females by visiting and inspecting female nesting sites very early on before dispersal of the groups (Radespiel 2000; Schmelting 2000; own observations). Furthermore, sometimes they even stay next to a nest waiting for a female and compete by fighting with other approaching males. During these turns they utter male mating advertisement calls, the trills. Laboratory studies revealed that these vocalisations were uttered most frequently by grey mouse lemur males when oestrous females were present, indicating their function in mate attraction / mate defence (Zimmermann and Lerch 1993).

Additionally, it was discovered only recently that the genus *Microcebus* contains a high diversity of cryptic sibling species, which occur sympatrically in several areas of Madagascar (Yoder et al. 2000; Kappeler et al. 2005; Olivieri et al. 2006 submitted). Therefore, it can be assumed that these calls may not only serve a purpose for attracting mates within the species, but, may also have an important function for species discrimination to avoid misdetection of potential mates on the basis of visual body characteristics.

For three species of mouse lemurs species-specific male mating advertisement calls have been documented. These showed obvious differences in their time-frequency contour: for the grey mouse lemur (Zimmermann and Lerch 1993; Hafen 1998), for the golden-brown mouse lemur (Polenz 2000) which occurs sympatrically to the grey mouse lemur and for the Goodman's mouse lemur (Zimmermann et al. 2000) which occurs allopatrically to the two other species. The first two mentioned species occur in dry deciduous forests of Madagascar where the grey species is widely distributed from the north-west to the south. The golden brown species is restricted to an area around the National Park of Ankarafantsika in the north-west of the island. Goodman's mouse lemurs are found in rain forest areas in the east of Madagascar.

As suggested (e.g. Ganzhorn et al. 1999) morphometric differences and niche differentiation is slight between the genetically distinct but closely related sympatric mouse lemur species. Individuals of the grey and the golden brown mouse lemur weigh about 60g and differ only in a few morphological parameters such as pelage colour, tail and limb length (Zimmermann et al. 1998). They also differ in the composition of sleeping groups, the preferred quality of sleeping sites and their reaction to disturbances at the sleeping site (Weidt et al. 2004; Radespiel et al. 2003a; Rendigs et al. 2003). Apart from this they share the forest strata, food resources and activity patterns.

For these reasons, the recognition of conspecifics in these small, cryptic species seems to be quite difficult. In several primate species advertisement or long calls showed species-specific signatures, which have been extensively used in taxonomic and phylogenetic studies (e.g. colobus monkeys: Oates et al. 2000; galagos: Zimmermann et al. 1988; Zimmermann 1990; Bearder 1995; gibbons: Mitani 1987; Geissmann 2002; tamarins: Masataka 1986; tarsiers: Nietsch and Kopp 1998). As mentioned above, the advertisement calls of mouse lemurs showed a species-specific call structure as well, providing a high potential for species recognition and discrimination, especially in sympatric species.

There is no guarantee that acoustic features that are obvious to a human observer in a spectrogram are behaviourally meaningful to a non-human primate (Owren and Linker 1995). Therefore one aspect of this thesis deals with a playback experiment to investigate the biological significance of species-specific advertisement calls in mouse lemurs and its impact as a potential premating isolation mechanism.

3.7 Aim of the study

The aim of the presented study was to gain further insights into the evolution of acoustic communication within the primates. Therefore, the variability and biological significance of social communication signals on the inter- and intra-species level in nocturnal primates of the same ecological community was investigated using sportive and mouse lemurs as models.

All three study species are solitary ranging but form individualised long-term sleeping associations, representing an intermediate condition between a solitary and a gregarious social system, as it is found in most anthropoid primates. The differences even in the characteristics of the social systems of the study species offer interesting aspects of adaptive evolutionary constraints. Furthermore, the sympatry of species, especially that of the two mouse lemurs, provides conditions for the study of the impact of species-specific acoustic communication in the light of diversification and speciation in these ancestral primates.

The aspect of **intra-specific** variation in communication was examined in two different nocturnal lemur species in order to illuminate the effect of sociality. The spacing between and coordination within mixed-sexed groups of golden brown mouse lemurs on the one hand (chapter 4) and pair-bonded Milne Edwards’ sportive lemurs on the other hand (chapter 5) was studied under natural conditions in the field. Before this thesis only anecdotal information was available concerning dispersal and group re-aggregation behaviour and the impact of acoustic signals during this period of time in solitary ranging primates (reviewed in Bearder et al. 2003).

For this aspect, first, radio-telemetry data should reveal if individuals use overlapping feeding or sleeping sites or both exclusively with respect to conspecific neighbours, thus, monopolising potentially restricted resources. Second, it should be clarified to what extent communication signals used by the individuals regulate inter- group spacing and / or intra-group cohesion in view of social structure and behaviour.

It was expected that vocalisations may facilitate the re-aggregation of the pair- or group-bonded individuals, which are dispersed in space. The quality and quantity of vocalisations occurring during dispersals and reunions should give information about the relevance of acoustic signals for intra- and inter-group concerns. Potential gathering calls are expected to carry individual-, sex-, pair- or group-specific call signatures, which may provide a means for pair and group recognition and discrimination.

The significance of variation on the **inter-specific** level was studied in mouse lemurs to explain general principles and species-specific adaptations of acoustic information processing (chapter 6). The aim of this part of the study was to examine whether the advertisement calls of the grey, the golden brown and Goodman’s mouse lemur were sufficiently different to be able to represent a premating isolation mechanism and may thus play an important role in speciation processes.

A prerequisite for such a mechanism is the production of species-specific signals and the perception of them as species-specific as was already shown for bats (Barlow and Jones 1997) and birds (de Kort and ten Cate 2001). In comparison to the advertisement calls, another call type - the short whistle call - should be tested for species-specific perception. This call is used in attention and alarm contexts (Scheumann et al. in press) and has not shown any statistical differences in structure between the three species (Zimmermann et al. 2000; Zietemann 2001).

Therefore, the biological significance of different levels of structural variation of vocalisations between species was studied experimentally by playback experiments with grey mouse lemurs from the field. These were tested with the contextually comparable species-specific advertisement calls and the inter-specifically similar alarm calls of its own, its sympatric and the mentioned allopatric species.

In synthesis I will discuss the acoustic variability of communication sounds in the two species of mouse lemurs and the Milne Edwards’ sportive lemur and present some aspects on the biological relevance of acoustic signals on the inter- and intra-specific level. The results will be presented with regard to speciation processes and the evolution of different social systems in the face of acoustic communication.

Finally, some aspects referring to the evolution of long distance calls in primates will be discussed in consideration of the obtained results of this thesis. The implementation of long distance calls in diurnal non-human primates will be presented in the light of potential ancestral signals as found in more primitive primate species represented by the studied nocturnal lemur species. In conclusion, the impact of acoustic communication for the evolution of higher primate societies will be discussed briefly.

4 Study 1

Spacing and group coordination in a nocturnal primate, the golden brown mouse lemur (*Microcebus ravelobensis*): the role of olfactory and acoustic signals*[1]

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 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 three to 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.

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4.1 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 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 60g, are omnivorous and show similar feeding habits (Radespiel et al. 2006 submitted), 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. Secondly, 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 1995a). 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. Thirdly, we hypothesised that vocal signals for group reunion carry long-term group-specific signatures which may provide a means for group recognition and discrimination.

4.2 Methods

4.2.1 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, north-west 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 years, spacing data in 2001.

We studied five sleeping groups of the golden brown mouse lemur, three of them in both 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 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 (c.f. 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 are given in Table 4-1.

Table 4-1: Representation of studied groups in the data sample[1].

	YEAR 2000*				**YEAR 2001**				
group	study animal	collar	***comm. signals***	***group-sp. trill sign.***	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				

[1]: comm. signals: communication signals, group-sp. trill sign.: group-specific trill signatures, ss: sleeping site, F: female, M: male, tr: transmitter, ref: reflective collar, *: these groups were also part of the study Weidt et al. 2004.

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 meters 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 one hour 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 were compared using the chi-square test. Small sample sizes were adjusted by the Yates method (Zöfel 1992).

4.2.2 Marking behaviour

We distinguished two types of marking behaviour (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.

4.2.3 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 seconds 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. 4-1), according to Zimmermann (1995a) and Zietemann (2001) by visual inspection of the sonagrams. Between these categories there were no transitions.

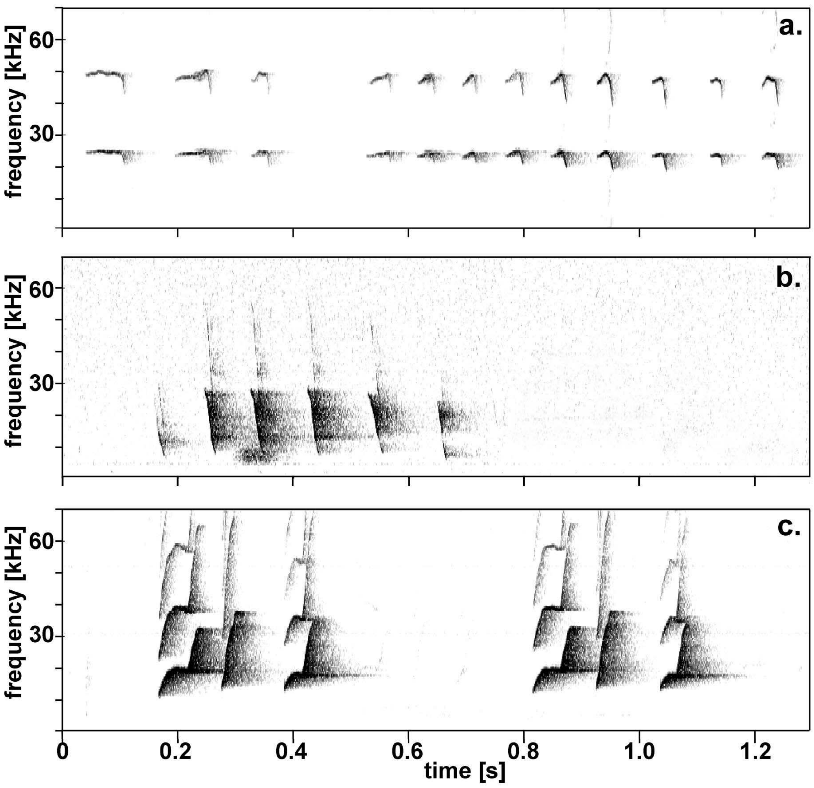

Fig. 4-1: Spectrograms (FFT size 512, Hanning window) of: a. whistles which turn into tsaks, b. wide-band zips and c. two trills consisting of three elements each.

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 (gr. 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 4-2): temporal parameters were determined using the waveforms, frequency parameters from the power spectra (BatSoundPro 3.0).

Table 4-2: Acoustic parameters of trills[2].

acoustic parameter	**description**
total call	
el	number of elements per call
f_0 start 1 [kHz]*	start frequency of the fundamental of element 1
f_0 end [kHz]*	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]*	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 [%]*	relative temporal position of minimum: 100 / call dur x dur min
pos f_0 max [%]*	relative temporal position of maximum: 100 / call dur x dur max
elements of the call	
f_0 start 2 [kHz]	f_0 start of element 2
f_0 end 1 [kHz]*	f_0 end of element 1
f_0 end 2 [kHz]*	f_0 end of element 2
band 1 [kHz]*	bandwidth of element 1: f_0 max of element 1 – f_0 min of element 1
band 2 [kHz]*	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]*	duration of element 1
dur 2 [ms]	duration of element 2
int 1_2 [ms]*	interval between onset of element 1 and onset of element 2

[2]: *: variable which remained after the Spearman-Rank-Correlation for the discriminant function analysis.

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 eleven 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.). Secondly, 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.

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).

4.3 Results

4.3.1 Spacing

Sleeping groups used between three to 17 sleeping sites in 2001. The groups changed their sleeping site every two to nine days (median=three days). We found the sleeping groups in 98% on average of all sleeping site localisations during daytime (c.f. Table 4-1). Sleeping sites were occupied exclusively, i.e. there was no case in which a group slept at a sleeping site of another group (Fig. 4-2). Due to predation or transmitter problems, we lost several study animals and in two cases the whole sleeping group after 41 and seven days (gr. 1 and 2), respectively.

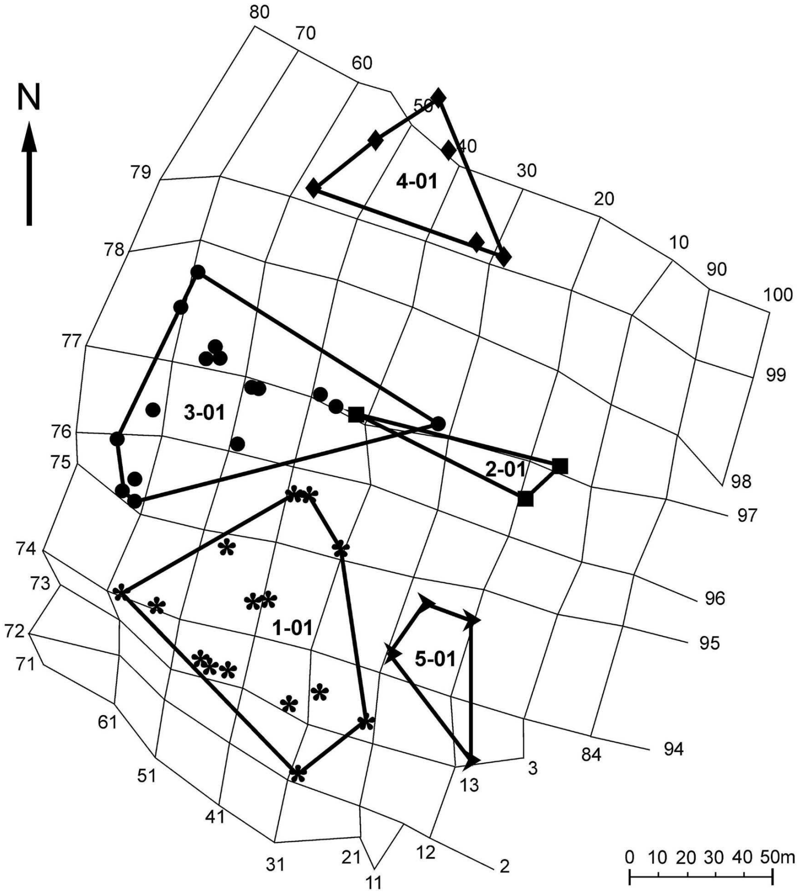

Fig. 4-2: Distribution of sleeping sites of the five groups in 2001. At the study site JBB a grid system was established. 100% minimum convex polygons are indicated by bold lines.

4.3.2 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.

4.3.3 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.

4.3.4 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, n.s.).

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.

4.3.5 Context of acoustic signals

The behavioural context in which whistles/tsaks and wide-band 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 two 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 a 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 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).

4.3.6 Trill structure

Trills consisted of two to six harmonically structured syllables or elements (Fig. 4-1). 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 to 400 ms. Minimum frequencies of the fundamental ranged from 9 - 18 kHz, maximum frequencies of the fundamental from 28 to 50 kHz. For the eleven acoustic parameters used for a detailed analysis (see “group-specific signatures of trills”) we present medians in Table 4-3.

Table 4-3: Selected acoustic variables from 81 trills of four sleeping groups (for parameter definitions see Table 4-2). 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

4.3.7 Group specific signatures of trills

The stepwise forward discriminant function analysis used six 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 4-4).

Table 4-4: Acoustic variables which were entered in the discriminant function analysis. 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.

variable	entered at step	Wilks-Lamda	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	.098	38.761	.186	.452	.604*	-.385
call dur	2	.068	19.260	.793	.257	-.654*	.605
band 1	3	.051	9.049	.561	-.320	-.005	.850*
dur 1	4	.059	13.677	.299	-.082	-.617*	.291
pos min	5	.046	5.579	.667	-.0.27	.266*	.070
f_0 end	6	.045	4.806	.867	.165	.287	.344*

92.6% of cross-validated cases of the year 2001 were classified correctly and 73.6% of the trills from the year 2000 were allocated to their respective group of 2001 (Table 4-5). A chi-square test revealed that this distribution is significantly different from chance in each group (gr.1: χ^2=46.67, p<0.001; gr.2: χ^2=9.0, p<0.029; gr.3: χ^2=19.89, p<0.001). Thus, trills provided sufficient information to discriminate between neighbouring groups in our study area.

Table 4-5: 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 (gr. 1-01 – 4-01) were cross validated (A). Trills of the year 2000 (gr. 1-00 – 3-00) were classified as new cases (B)[3].

	% 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

[3] : “n”: number of trills included in the analysis per group.

4.4 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 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.

4.4.1 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; 2003a), 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.

4.4.2 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.

4.4.3 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 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 summarized 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 one 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. Secondly, 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.

4.4.4 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).

4.5 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.

5 Study 2

Loud calling, spacing, and cohesiveness in a nocturnal primate, the Milne Edwards' sportive lemur (*Lepilemur edwardsi*)*[2]

Dispersed pair-living primates provide a unique model for illuminating the evolution of mechanisms regulating spacing and cohesiveness in permanently cohesive groups. We present for the first time data on the spatio-temporal distribution and on loud-calling behaviour of the Milne Edwards’ sportive lemur, known to forage solitarily during the night, but to form stable male-female sleeping groups during the day. Data include radio-tracking observations of sleeping associations and focal follows of pair partners during dispersal in the evenings and reunions in the mornings. Male-female pairs forming stable sleeping associations during the day were pair-bonded. They used sleeping sites and home ranges exclusively, and exchanged loud calls at potentially restricted resources during dispersal in the evenings and during reunion in the mornings. Direct agonistic conflicts between pairs and others were rare. The acoustic analysis of loud calls revealed nine major call types. They carry signatures for sex and pair identity and provide the substrate for signalling and the potential for recognizing pair ownership. Thus, pairs use loud call exchanges as a vocal display for signalling territory ownership, thus limiting direct aggressive encounters between neighbours and strangers. Altogether our findings provide first empirical evidence for the hypothesis that loud calling has evolved as a key mechanism for regulating space use and cohesiveness in dispersed pair-living primates.

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*[2] ***puplished as***: Rasoloharijaona, S.; Randrianambinina, B.; Braune, P.; Zimmermann, E. (2006) Loud calling, spacing and cohesiveness in a nocturnal primate, the Milne Edwards’ Sportive lemur (*Lepilemur edwardsi*). Am. J. Phys. Anthropol. 129: 591-600; Copyright ©2006 John Wiley & Sons, Inc. Reprinted with permission of wiley-Liss, Inc. a subsidiary of John Wiley & Sons Inc.

5.1 Introduction

Loud or long distance calls are common across taxa as diverse as insects, fish, frogs, birds and mammals (e.g. Zimmermann et al. 1995; Ryan and Kime 2003). Whereas loud calls are used primarily in the mating context to attract potential mates and repel rivals and thus increase reproductive success in solitary living invertebrates and lower vertebrates without long-term social bonds (e.g. Ryan and Kime, 2003). Their function in societies of group-living, permanently bonded individuals is much more complex. Functional explanations for loud calling behaviour in permanently cohesive, anthropoid primates have implied a role in predator perception, predator advertisement, food advertisement, group re-aggregation and resource defence (e.g. Gautier and Gautier 1977; Waser and Waser 1977; Wrangham 1977; Sekulic 1982a, b; Mitani 1985a; Cheney 1987; Whitehead 1987; Brown 1989; Hohmann and Fruth 1995; Boinski and Garber 2000; Wich and Nunn 2002).

Individuals in all anthropoid primates (with the exception of orang-utans) live in permanently cohesive social groups (e.g. Fleagle 1999; Kappeler and van Schaik 2002). In contrast, strepsirrhine primates show a broad diversity in social patterns (e.g. Müller and Thalmann 2000). This makes them a unique model for assessing the significance of vocal behaviour in regulating inter-group spacing and intra-group cohesion in primates. However, empirical studies focusing on this aspect in nature are rare.

Bioacoustic studies on nocturnal solitary foraging strepsirrhine primates in captivity suggest that loud calls are used in both males and females for sexual advertisement in the mating context, in accordance with the mate attraction/mate defence hypothesis (Zimmermann and Lerch 1993; Buesching et al. 1998, Hafen et al. 1998). The species-specific distinctiveness of these calls (Zimmermann et al. 1988, 2000; Zimmermann 1990; Bearder et al. 1995; Anderson et al. 2000; Ambrose 2003), and their species-specific recognition (Braune et al. 2004) imply their importance for sexual selection and speciation. Indeed, a first experimental study (Craul et al. 2004) on captive grey mouse lemurs (*Microcebus murinus*) showed that a sexual advertisement call, the trill, functions as a potential candidate for female mate choice.

Likewise, a first quantitative field study in the golden brown mouse lemur (*Microcebus ravelobensis*) living in a dispersed multimale-multifemale system with stable, mixed-sexed sleeping groups of up to five adult members provides first empirical evidence that a structurally similar call is used for group re-aggregation and co-ordination (Braune et al. 2005, see chapter 4). Until now, empirical field studies illuminating the role of loud calling for spacing and cohesion in taxa in which individuals forage solitarily during the night, but gather to form stable, male-female sleeping groups during the day, are lacking.

The Milne Edwards’ sportive lemur provides an excellent model to gain insight into the underlying mechanisms regulating spacing and cohesiveness in permanent cohesive groups. It is a 930-g nocturnal prosimian primate that feeds mainly on leaves and forages solitarily (Thalmann and Ganzhorn 2003). In contrast to a variety of other lemurs, this species is highly vocal, but does not show any marking behaviour (Rasoloharijaona et al. 2003). Sexes are sexually monomorphic and do not differ in either body size or body mass.

Recent radio-telemetric studies revealed that one adult male and one adult female form a stable and long-term sleeping association using potentially restricted resources such as safe sleeping sites exclusively (Rasoloharijaona et al., 2003). A study on the home ranges of one radio-collared female and one male furthermore suggested territoriality (Thalmann and Ganzhorn, 2003). Likewise, Rasoloharijaona et al. (2000) witnessed one case of infanticide by a male stranger when a female slept together with a baby and an older offspring, but without an adult male, suggesting that a female may profit from an association with a male because of better offspring protection.

The goal of this paper is to test the following three hypotheses. First, male-female sleeping associations of the Milne Edward’s sportive lemur are pair-bonded. Pairs monopolise potentially restricted resources for (e.g., sleeping sites or space for foraging) by exclusive usage. Second, loud calling functions as a co-operative display of territory defence. A pair organized as a sleeping association during the day shows joint loud calling activity at potentially limited resources in their home range before dispersal in the evenings and at reunion in the mornings. Direct agonistic conflicts between the pair and neighbours and strangers at these sites are rare. Third, the acoustic structure of loud call sequences provides the substrate for signalling pair ownership to neighbours and strangers. Loud call structure conveys individuality and as a consequence is different between pairs.

5.2 Methods

5.2.1 Study site and animals

We performed the study in the western Malagasy dry deciduous forest in the Réserve Forestière d’Ampijoroa (16°19’S, 46°49’E), located about 110km southeast of Mahajanga. For a detailed description of the forest and climate conditions see Rendigs et al. (2003).

The study took place from May until November 1998 and from May until November 2001 at two study sites locally known as “Jardin Botanique A (JBA)” and “Jardin Botanique B (JBB)”. Lemurs were captured at the onset of their activity period with a mist net, fastened around the sleeping hole, or with a blowpipe using 1ml cold air pressure narcotic syringe projectiles with the Oversea set from Telinject (Germany). We used Ketasel 50 (50mg Ketasel/ml) in the dose recommended by the manufacturers as anesthetic. The lemurs were briefly anaesthetised for measurement, marking and equipment with a radio-collar and released after recovery at their capture site late in the same night. Sleeping sites were reused by the same individuals on the forthcoming day showing that the procedure did not noticeably harm them. Radio-collars were removed at the end of the respective study period. All procedures were carried out with permission of the Malagasy Government.

In 1998, we radio-collared 4 males and 3 females via TW-3 button-cell tags (Biotrack, Dorset, UK) in JBA, and 2 males and 3 females in JBB. In 2001, we radio-collared 5 males and 6 females in JBA (see Table 5-1). All lemurs were marked individually by cutting patterns into the hair of their tails. The lemurs were aged as adult or non-adult according to body length (Rasoloharijaona et al. 2003).

Table 5-1: Sleeping associations and sites used (partners together indicate the number of days at which pairs were found together related to the total number of days at which individuals were localised).

Pair code	**Family**	**Number of sites**	**Partners together**	**Percentage together**
F0197-M0998	1	2	8/76	10.53
F0798-M0898	2	4	67/76	88.16
F0598-M1598	3	3	16/47	34.04
F1298-M1398	4	3	48/50	96
F1798-M1898	5	2	1/22	4.55
F0501-M0101	6	3	49/59	83.05
F0601-M0201	7	2	26/57	45.61
F0701-M0501	8	2	29/30	96.66
F1001-M0301	9	2	3/27	11.11

5.2.2 Data collection and processing

Sleeping associations of radio-collared lemurs were determined between May and November 1998 and May and November 2001 on the basis of telemetric localisations of radio-collared animals during the day and additional observations at the sleeping site at dusk and dawn. The sleeping sites were numbered and marked on a map. Male-female pairs which slept together were defined as a sleeping group. According to this criterion, nine females and nine males were defined as sleeping pairs (Table 5-1). For the other two males and three females we did not succeed in capturing their respective partners. We counted all used sleeping sites per individual.

For July (after the mating season) and October (birth season) 2001, home range sizes, locations, and home range overlaps of all radio-collared lemurs of 2001 were determined telemetrically according to Radespiel et al. (1998) and Radespiel (2000). A portable TR-4 receiver and a RA-14K antenna (Telonics, Inc., Impala, AZ) were used. The triangulation data points of an individual were collected at intervals of a minimum of 30 min during sessions lasting approximately 6 hr per night. In general, triangulation sessions took place alternately, in the first and second half of the night, for 6 nights in each telemetric period.

In total, 60 data points were collected per animal. Home ranges were analysed using Trackasc (software A. Ganzhorn, 1996, unpub.) and Ranges V software (software, Institute of Terrestrial Ecology, Wareham, UK; Kenward, 1990), and were calculated as minimum convex polygons (White and Garrott 1990) on the basis of 100% of the data points. Mean home range sizes were compared between sexes and seasons. Mean home range overlaps were calculated intra- and inter-sexually for all possible dyads of radio-collared animals, considering overlaps in both directions.

Direct focal observations were carried out on all radio-collared individuals in 1998 and 2001, using focal animal sampling with continuous recording (Altmann 1974a; Martin and Bateson 1993) simultaneously by two observers for one hour after the individuals left their sleeping sites during the evenings (dispersal) and for one hour before they returned to them during the mornings (reunion). Lemurs were observed by dimmed light using headlamps. Social behaviours, and additional information related to spatial and ecological factors (e.g., location within the home range, climate conditions) were recorded on a Dictaphone and subsequently transferred to data sheets.

Social encounters were defined as meetings with one or more conspecifics at a time within the 5-m range of the focal animal during the activity period at night. A social encounter was defined as an agonistic conflict whenever fighting, hitting, biting, chasing, or fleeing occurred. An affiliative contact between lemurs was defined as when locomotion or sitting in body contact or sitting within 1-m from each other without any agonistic behaviour, sniffing without successive agonistic behaviour, or social grooming occurred. Loud calling between pair partners occurred mainly during social encounters at feeding and sleeping sites. There was only one direct agonistic conflict between a male of one of our pairs and a stranger in the vicinity of the pairs sleeping site which we excluded from our analysis because of the low sample size. No predator-lemur interaction occurred during our observations.

For analysis, we established seven call-related behavioural contexts and recorded their occurrence for each observation session: contact at the feeding site, conflict at the feeding site, contact at the sleeping site, conflict at the sleeping site, travelling, sitting alone at the sleeping site and unknown context (loud calls of radiotracked individual heard, but individual out of sight). One to eight morning (2.92 ± 2.64) and one to eight evening sessions per animal (2.83 ± 2.28) were included. We counted the number of evening and morning sessions in which the context was present as well as the number of pairs involved.

All sound recordings were made with Sony Super Chrome Class UX-S IECII/Type II tapes using a Sony WM-D6C Professional Walkman cassette recorder and a Sennheiser ME 88 directional microphone. Because the animals were habituated to researchers and their equipment, high-quality recordings could be made at relatively close range (3-5 m).

Recordings of loud calling sessions from all the animals were used to determine the major call types exchanged during social encounters. Nine different call types (Fig. 5-1) were discriminated on the basis of digitized recordings and visual inspections of the sonograms. For assessing acoustic cues for individual identity, high quality recordings of vocal exchanges between the pairs of 1998 were used. Temporal and source-related acoustic features of call types were extracted using AviSoft SAS LabPro (Specht, 1996, FFT size: 512, Hanning window; see Table 4-2 for explanation).

Table 5-2: Acoustic parameters measured from waveforms and spectrograms.

Acoustic parameter	Description
Source related	
Fo start [kHz]	start frequency of the fundamental (Fo) of element 1
Fo end [kHz]	end frequency of Fo of element 1
Fo end 2 [kHz]	Fo end of element 2
Fo max 1 [kHz]	Maximum frequency of Fo of element 1
Fo max 2 [kHz]	Maximum frequency of Fo of element 2
BW 1 [kHz]	Bandwidth 1 (Fomax-Fostart)
BW 2 [kHz]	Bandwidth 2 (Fomax-Foend)
BW 3 [kHz]	Bandwidth of first frequency modulation of Fo within the call
Temporal related	
D 1 [ms]	Duration between start and maximum frequency of Fo
D 2 [ms]	Duration between maximum frequency and end frequency of Fo
Dur total [ms]	Total call duration
dur 1 [ms]	duration of element 1
dur 2 [ms]	duration of element 2

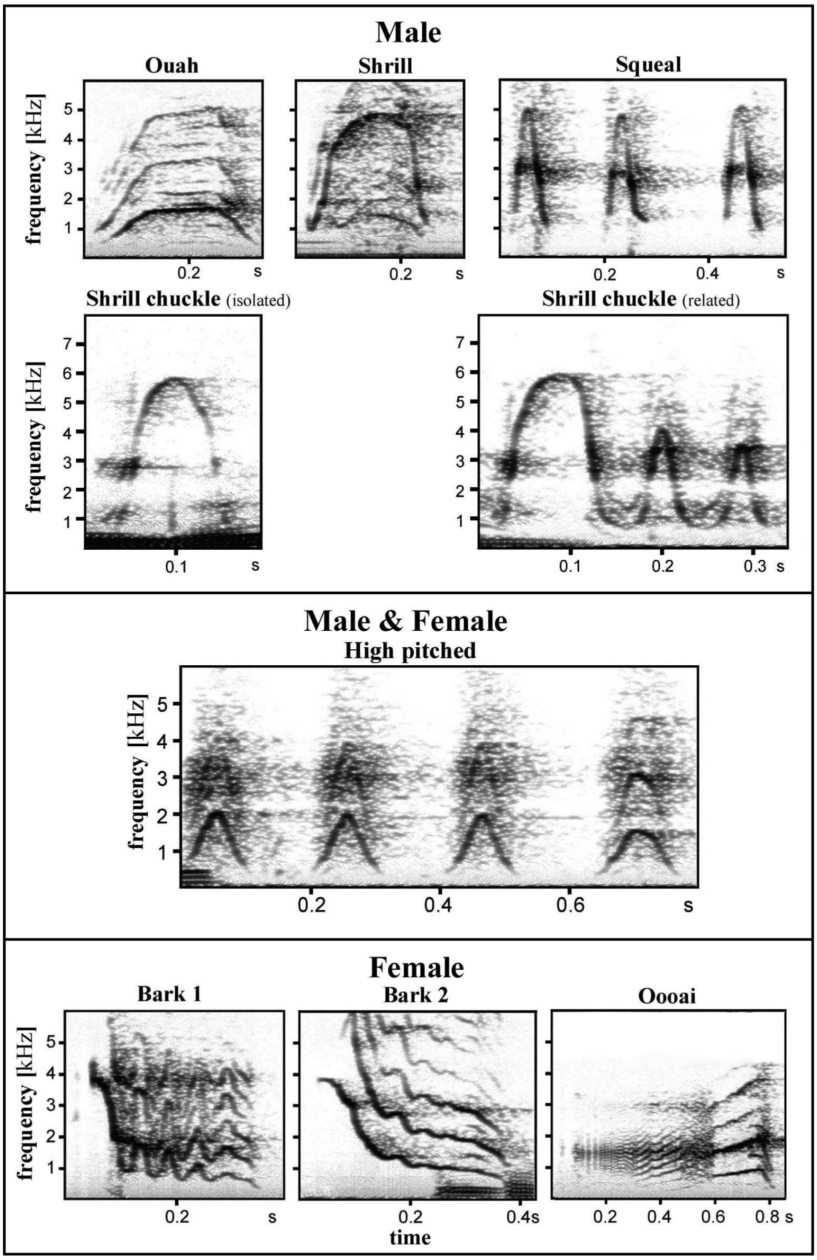

Fig. 5-1: Sonograms of common and sex-specific syllables of loud calls in the Milne Edwards' sportive lemur.

5.2.3 Statistical analysis

Comparisons between two dependent data sets were conducted with the Wilcoxon matched-pairs test. Independent data sets of males and females were compared with the Mann-Whitney U-test. For all statistical procedures of the univariate statistics see Sokal and Rohlf (1981). All tests were two-tailed, with an overall level of significance of P < 0.05. Statistica Version 5 (Statsoft) was used for all univariate statistics.

Chi-square tests were used to compare the presence of the particular call-related context between evening and morning sessions. Low sample sizes were adjusted by the Yates method (Zöfel, 1992).

Medians and interquartile ranges were calculated for the four major acoustic parameters characterizing each call type (Fostart, Fomax1, Foend, Dur total; see Table 5-2). We used a discriminant function analysis for each call type to investigate if it encoded individually specific signatures. Parameters which characterised the respective call structure 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 respective discriminant function analysis. Parameter pairs with $r_s<0.75$ were defined as non-related (SPSS 11.0, SPSS, Inc.). The latter formed the basis for the discriminant function model of each call. For model calculations, we used the stepwise forward method (statistic: Wilk's-λ) with the criteria $F_{to\ enter}=3.84$ and $F_{to\ remove}=2.71$ and a tolerance level of ≤ 0.01 to calculate the discriminant function model (SPSS 11.0, SPSS, Inc.). Results were cross-validated by the "leave-one-out" method, where each case of the analysis was classified by the functions derived from all cases other than that case (SPSS 11.0, SPSS, Inc.). For this classification a priori probabilities were dependent on group size, because different number of calls per group formed the basis of the model.

5.3 Results

5.3.1 Sleeping associations

Milne Edwards' sportive lemurs used tree holes in dead or live trees for sleeping (except for one case of a leaf nest) during the day and shared them regularly with a pair partner in six of nine studied pairs (Table 5-1). In four of them, pair partners slept together for more than on average 90% of localisation days. Partners either slept together in the same hole or in different holes of the same tree or in holes of two trees in the vicinity. The number of sleeping sites used by an adult individual was 1 to 4. Sleeping sites were never shared with neighbours, neither simultaneously nor consecutively.

5.3.2 Home ranges and overlap

Home range size was 0.98±0.4 ha for females and 1.01±0.25 ha for males. There was neither a sex (Mann-Whitney U test: U=12, $N_m=5$, $N_f=6$, NS) nor a seasonal difference in home range sizes (Wilcoxon signed-ranks test: T $_{\text{july vs. october}}$= 32, N=11, NS). Home ranges of females overlapped with those of all neighbouring females by a median of 6.1 % in July and 4.9% in October. Male-male home range overlap was slightly lower with 2% in July and 4.9 % in October. The home ranges of sleeping partners overlapped extensively in form and size (male: 69.4 % in July and 68.1 % in October, female: 82.7 % in July and 87.5 % in October, Fig. 5-2). Sleeping pairs used their common home range almost exclusively.

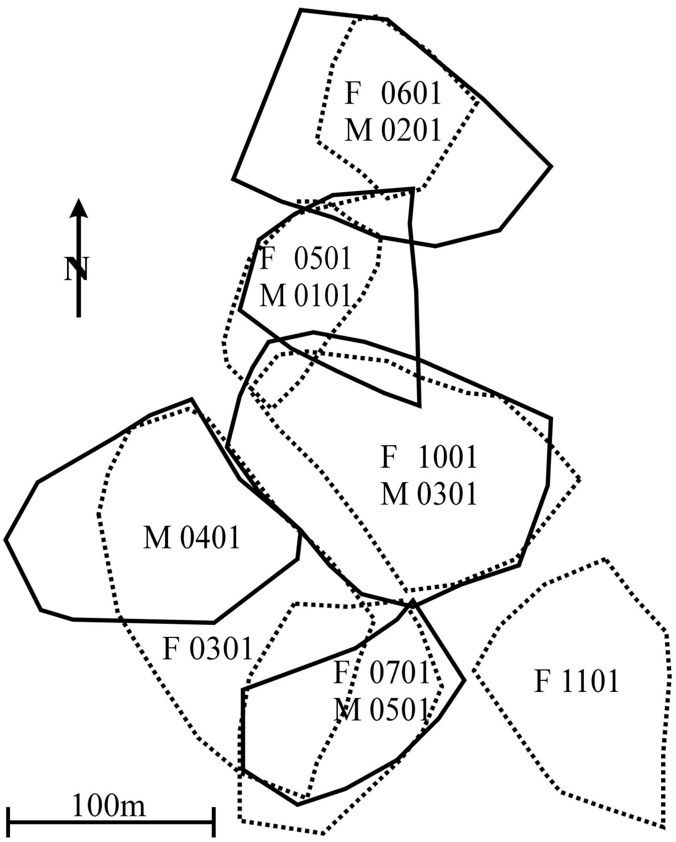

Fig. 5-2: Minimum Convex Polygons of ranges of adult individuals in October 2001. Dotted outlines: female ranges; bold lines: male ranges. The male of female 11-01 was never captured. Female 03-01 and male 04-01 shared the same range, but not the same sleeping tree or sleeping trees in the vicinity and were therefore not treated as a pair.

5.3.3 Loud calling behaviour

During 68 hours of direct visual contact with an adult focal animal, 98 loud calling events between pair partners were observed (Table 5-3). All nine pairs exchanged loud calls during the mornings (N=34), and all except one pair during the evenings (N=34). Focal animals showed loud calling behaviour in seven different behavioural contexts, most of them associated with either feeding or sleeping sites. During the evenings, 50.9% of loud call events (N_{total}=55) were related to sleeping sites and 38% to feeding sites, whereas during the mornings, they were primarily related to sleeping sites (76.7%, N_{total}=43). 38.8% of all loud calling events accompanied pair conflicts over these sites. Whereas loud calling events at the feeding site did not differ between evenings and mornings, loud calling events related to conflicts over the sleeping site occurred significantly more often during the mornings (χ^2-test, Table 5-3).

Table 5-3: Context of loud calling events in nine pairs during evening (N=34) and morning sessions (N=34)[4].

Context	**Evenings** n_s	n_p	**Mornings** n_s	n_p	**χ^2 (E/M)**	**P**
Feeding site, contact	11	7	4	4	3.08	P<0.079 NS
Feeding site , conflict	10	5	3	3	3.42	P<0.064 NS
Sleeping site, contact	13	8	10	7	0.55	P<0.441 NS
Sleeping site, conflict	6	3	19	5	10.69	P<0.009
Sleeping site alone	9	3	4	2	1.52	P<0.217 NS
Travelling	2	2	2	1	-	-
Unknown	4	3	1	1	-	-
Total $n_{context}$	55		43			

[4]: n_s= number of sessions in which the respective context occurred, n_p=number of pairs for which the respective context was noted, NS: not significant.

5.3.4 Sex and individual identity in loud calls

Loud calling consists of sequences of a total of nine structurally different call types (Fig. 5-1), of which most were sex-specific: one call type, the high pitched call (HPC), was shared between the sexes, three call types were used only by females (bark 1, bark 2, oooai) and five only by males (ouah, shrill, squeal, shrill chuckle (isolated), shrill chuckle (related)). Table 5-4a, b presents medians and quartiles for acoustic parameters of each call type. As all call types may be present in different contexts, we investigated to what extent they carried individual-specific signatures in source or temporal related features by applying a stepwise forward discriminant analysis.

Table 5-5 a, b shows the selected variables which formed the basis for the discriminant analysis for each sex-specific call type, those which were used for the respective model calculation, the model parameters and their significance.

Table 5-4a: Descriptive statistics for major acoustic variables measured in the six different call types used by males.

Call type n (call) N (individual)	**OUAH** 39 3			**SHRILL** 126 4			**SQUEAL** 85 3		
	median	lower quartile	upper quartile	median	lower quartile	upper quartile	median	lower quartile	upper quartile
F_0 start [kHz]	0.703	0.609	0.750	0.914	0.773	1.289	1.359	1.172	2.063
F_0 max 1 [kHz]	2.109	1.688	2.438	4.863	4.547	5.156	4.477	3.188	4.828
F_0 end [kHz]	0.703	0.656	0.773	0.891	0.773	1.031	0.867	0.773	0.984
Dur total [ms]	0.271	0.232	0.289	0.190	0.160	0.211	0.075	0.051	0.093
Call type n (call) N (indiv.)	**SCC** 105 4			**SHCC** 124 4			**HPC** 52 3		
	median	lower quartile	upper quartile	median	lower quartile	upper quartile	median	lower quartile	upper quartile
F_0 start [kHz]	0.781	0.688	0.875	0.781	0.688	0.875	0.633	0.551	0.727
F_0 max 1 [kHz]	4.250	3.844	5.531	5.641	5.266	6.031	1.219	1.066	1.430
F_0 end [kHz]	0.750	0.656	0.813	0.688	0.594	0.750	0.633	0.516	0.750
Dur total [ms]	0.093	0.059	0.130	0.285	0.262	0.331	0.048	0.043	0.055

Table 5-4b: Descriptive statistics for major acoustic variables measured in the four different call types used by females.

Call type n (call) N (individual)	**BARK 1** 47 3			**BARK 2** 93 4		
	median	lower quartile	upper quartile	median	lower quartile	upper quartile
F_0 start [kHz]	2.930	1.734	3.750	4.148	3.680	5.016
F_0 max 1 [kHz]	3.773	3.188	4.523	4.148	3.680	5.016
F_0 end [kHz]	0.656	0.586	0.727	0.680	0.609	0.773
Dur total [ms]	0.233	0.207	0.269	0.332	0.273	0.381
Call type n (call) N (indiv.)	**OOOAI** 95 3			**HPC** 194 6		
	median	lower quartile	upper quartile	median	lower quartile	upper quartile
F_0 start [kHz]	-	-	-	0.766	0.656	0.859
F_0 max 1 [kHz]	0.922	0.828	1.344	1.625	1.297	2.266
F_0 end [kHz]	-	-	-	0.578	0.516	0.672
Dur total [ms]	0.708	0.470	0.844	0.064	0.054	0.082

Table 5-5a: Acoustic variables included in the stepwise forward discriminant analysis and results for male call types.

call type		**OUAH**	**SHRILL**	**SQUEAL**	**SCC**	**SHCC**	**HPC**
Selected variables	1.	F_0 start	F_0 end	F_0 start	F_0 start	F_0 start	F_0 start
	2.	F_0 end	BW 1	F_0 end	F_0 end	F_0 end	F_0 end
	3.	BW 2	BW 2	F_0 max	BW 2	F_0 max 2	BW 1
	4.	Dur total	Dur total	Dur total	D 1	F_0 end 2	BW 2
	5.	D 1	D 1	D 1	D 2	BW 3	Dur total
	6.	D 2				Dur total	D 1
	7.					dur 1	D 2
	8.					dur 2	
Used variables	1.	D 2	D 1	Dur total	D 1	BW 3	BW 2
	2.	BW 2	Dur total	F_0 max	BW 2	F_0 max 2	BW 1
	3.	F_0 end	BW 2	D 1	D 2	dur 1	
	4.		F_0 end	F_0 end	F_0 start	F_0 end	
	5.		BW 1			dur 2	
Wilks-λ		0.354	0.008	0.48	0.65	0.017	0.134
F (last step)		7.72	105.24	70.09	39.18	73.08	41.56
Df1 / df2		6 / 68	15 / 326	8 / 158	12 / 260	15 / 320	4 / 96
Significance		< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001

Table 5-5b: Acoustic variables included in the stepwise forward discriminant analysis and results for female call types.

call type		**BARK 1**	**BARK 2**	**OOOAI**	**HPC**
Selected variables	1.	F_0max	F_0 start	F_0max	F_0 start
	2.	F_0 end	F_0 end	Dur total	F_0 end
	3.	F_0max 2	Fmax2		F_0max
	4.	F_0 end 2	F_0 end 2		Dur total
	5.	D 1	D 1		
	6.	Dur total	Dur total		
Used variables	1.	F_0 end	F_0 start	Dur total	F_0max
	2.	F_0max	Dur total	F_0max	Dur total
	3.	Dur total	F_0 end 2		F_0 end
	4.		F_0 max 2		F_0 start
	5.		F_0 end		
Wilks- λ		0.140	0.22	0.182	0.118
F (last step)		23.356	46.458	61.293	27.762
Df1 / df2		6 / 84	15 / 235	4 / 182	20 / 615
Significance		< 0.001	< 0.001	< 0.001	< 0.001

We yielded an amount of over 90% correct classification in two out of four female calls, and in three out of six male calls (Table 5-6 a, b). Both, source and temporal related variables accounted for individual discrimination within sexes.

Table 5-6a: Classification table of the discriminant function analyses for male call types.

	Ouah							**Shrill**							**Squeal**						
	% correct	to individual						% correct	to individual						% correct	to individual					
		1	2	3	4	5	6		1	2	3	4	5	6		1	2	3	4	5	6
cross validation	**69.2**							**96.8**							**91.8**						
M0998 (1)	**45.5**	***5***				2	4	**97.1**	***34***	0	0		1		**97.1**	***34***	1	0			
M1898 (2)								**96.9**	0	***31***	1		0		**84.4**	5	***27***	0			
M1598 (3)								**100**	0	0	***27***		0		**94.4**	0	1	***17***			
M0898 (4)																					
M1398 (5)	**62.5**	3				***5***	0	**93.8**	1	1	0		***30***								
M5198 (6)	**85.0**	3				0	***17***														
	Shrill Chuckle							**Shrill chuckle related**							**High pitched call**						
	% correct	to individual						% correct	to individual						% correct	to individual					
		1	2	3	4	5	6		1	2	3	4	5	6		1	2	3	4	5	6
cross validation	**81.0**							**96.0**							**78.8**						
M0998 (1)	**90.5**	***19***	0	0		2		**97.0**	***32***	0	0		1		**75.0**	***6***			2	0	
M1898 (2)	**91.4**	0	***32***	3		0		**100**	0	***25***	0		0								
M1598 (3)	**79.5**	1	7	***31***		0		**88.0**	2	0	***22***		1								
M0898 (4)															**68.4**	0			***13***	6	
M1398 (5)	**30.0**	7	0	0		***3***		**97.6**	1	0	0		***40***		**88.0**	0			3	***22***	
M5198 (6)																					

Table 5-6b: Classification table of the discriminant function analyses for female call types.

	Bark 1							**Bark 2**						
	% correct	to individual						% correct	to individual					
		1	2	3	4	5	6		1	2	3	4	5	6
cross validation	**91.5**							**96.8**						
F5098 (1)	**70.0**	***7***		2		1		**96.0**	***24***	0	1	0		
F1798 (2)								**85.7**	0	***6***	0	1		
F0598 (3)	**95.7**	1		***22***		0		**100**	0	0	***24***	0		
F0798 (4)								**97.3**	1	0	0	***36***		
F0197 (5)	**100**	0		0		***14***								
F1298 (6)														
	Oooai							**High pitched call**						
	% correct	to individual						% correct	to individual					
		1	2	3	4	5	6		1	2	3	4	5	6
cross validation	**66.3**							**64.4**						
F5098 (1)								**57.1**	***12***	1	2	4	2	0
F1798 (2)								**87.5**	0	***28***	0	0	0	4
F0598 (3)	**93.3**			***28***	2		0	**43.9**	6	0	***18***	2	4	11
F0798 (4)	**40.0**			0	***12***		18	**70.6**	0	1	6	24	1	2
F0197 (5)								**64.7**	0	1	6	4	***22***	1
F1298 (6)	**65.7**			1	11		***23***	**65.6**	0	1	3	4	3	***21***

The distribution of discrimination scores for the individually most distinctive call type (the shrill call in males and the bark 2 call in females) according to individuals is shown in Figure 5-3. High pitched calls showed the same overall frequency contour between sexes, but differed significantly in total call duration (Mann-Whitney U test: $U=0$, $N_m=3$, $N_f=6$, $p<0.02$). Calls of males were shorter than those of females.

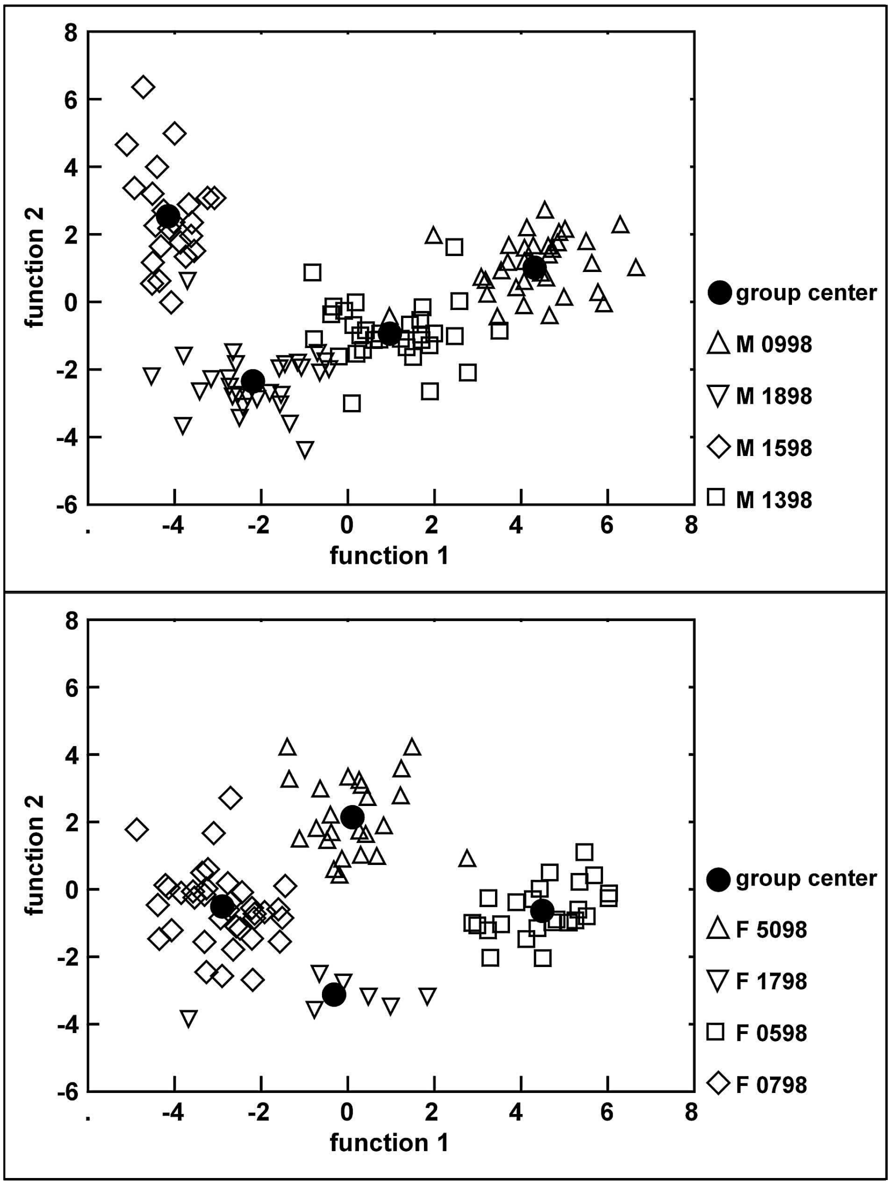

Fig. 5-3: Canonical variates of bark 2 calls of four different females (a) and of shrill calls of four different males (b) based on the first two canonical discriminant functions in the analysis that includes both source and temporal related acoustic variables.

5.4 Discussion

5.4.1 Spacing and cohesion within and between male-female pairs

Socio-ecological models imply that the spatiotemporal distribution of animals in space is related to the distribution of restricted resources (Emlen and Oring 1977; Clutton-Brock 1989). Since the fitness of females in mammals is more dependent on the access to restricted resources important for offspring survival (such as feeding or safe sleeping sites), while the fitness of males is more dependent on access to fertile females, the distribution of limited resources may predict group size, cohesion and movement patterns of animals (Trivers 1972; Clutton-Brock and Parker 1992; Wrangham et al. 1993; Dunbar 1994).

If feeding or safe sleeping sites show a defendable distribution, benefits for their defence may outweigh costs, and site-related territoriality may evolve (Kaufmann 1983). If fecundity of females is further on seasonally restricted to only a few weeks of the year and neighbouring females synchronise oestrus, a male may be forced to follow a single female throughout the whole year and defend her against rivals to guarantee reproductive success. Females should only tolerate males with whom they compete for food if they profit from a permanent association with a male, e.g., by defence of territories against rivals, by protection against infanticide, or by cooperation in paternal care (van Schaik and van Hooff, 1983; van Schaik and Kappeler 1997).

Our results on spacing behaviour support this model for Milne Edwards' sportive lemur and confirm the first hypothesis in the introduction. A heterosexual pair which forms a sleeping group shared the same space for foraging during the night. Pairs used sleeping sites and home ranges exclusively suggesting territoriality and favouring co-operative resource defence. Home ranges were small, at about 1 ha, confirming earlier studies on a smaller sample size in this species (Warren and Crompton 1997; Thalmann 2001). A similar pattern of spacing is found in dispersed pairs and in permanently cohesive pairs of other territorial primates (e.g., Müller and Thalmann 2000; Schülke and Kappeler 2003; van Schaik and Kappeler 2003).

Females of the Milne Edwards' sportive lemur show a seasonal reproduction of about one month from mid-May to mid-June and neighbouring females seem to synchronise oestrus (Randrianambinina et al., unpubl. data), as is common for lemurs (Radespiel and Zimmermann 2001). Furthermore, it is known that lemur females are fertile for only a few hours during their oestrus cycle (e.g., Wright 1999; Radespiel and Zimmermann 2001). This reproductive pattern in females as well as the low basal metabolic rate of nocturnal lemurs compared to anthropoids (Drack et al. 1999; Wright 1999) may force males into the guarding and defence of a single female, and may lead to permanent pair bonds. The relatively high degree of conflicts at feeding and sleeping sites among pair partners in three to five of our nine studied groups as well as the variability in time spent together by the studied pairs, warrants further examination with a higher sample size over a much longer duration. This degree of conflict does not seem to be related to the amount of co-sleeping in pairs (Rasoloharijaona and Zimmermann, unpubl. data), but might be associated with the strength of the male and female dominance (e.g., Rasoloharijaona et al. 2003) and thereby to the quality of the pair bond.

5.4.2 Functions of loud calling

Five hypotheses have been put forth in the literature to explain the occurrence of loud calling behaviour in primates. The predator perception/predator advertisement hypothesis (e.g. Cheney and Seyfarth 1990b; Hauser 1996; Zuberbühler 2003) assumes that loud calls function as warning signals in order to advertise predators. It predicts that loud calling activity is associated with predator-prey interactions. Since we did not see any predator-lemur interaction during our study, this hypothesis does not explain the occurrence of loud calls in our study. The food advertisement hypothesis (see references above) is not supported either, since loud calling is not only related to feeding sites in the Milne Edwards' sportive lemur.

The group-coordination hypothesis (Braune et al., 2005) suggests that loud calling helps individuals of a group dispersed in space to gather and to co-ordinate group movement. In groups, where individuals forage solitarily, but sleep together, it is expected that loud calling shows an asymmetrical temporal distribution (related to group reunion at dusk, but not to group dispersal at dawn). As our study revealed, there is no temporal asymmetry in the distribution of loud calling between evening and morning sessions. This indicates that loud calling in sportive lemurs does not function predominantly as a gathering call.

The mate attraction/mate defence and the resource defence hypothesis, which may be summarised in the territory defence hypothesis, are equally likely to explain the evolution of loud calling in sportive lemurs. These predict a symmetrical temporal distribution between morning and evening sessions and a strong relation of loud calling behaviour to potentially restricted resources such as feeding or sleeping trees, as supported by our data. Sportive lemurs live in dense, dry deciduous forests with limited visibility. Compared to anthropoid primates, visual acuity is low (Pereira 1995).

Likewise, in contrast to other nocturnal mammals, Milne Edwards' sportive lemurs do not show any sign of scent or urine marking behaviour; nor do they possess any specialised glands (Hill 1953; Petter et al. 1977). With an average nightly path length of 343 m (Warren and Crompton 1997) compared to a home range size of 1 ha, home ranges used exclusively by the same pair should be defendable. Direct agonistic interactions between neighbouring pairs, however, were rare during our whole observation period. Pair partners, however, showed a prominent loud calling behaviour at potentially limited resources such as feeding and sleeping sites, heard over a distance of more than 500 m and thus extending far into the neighbouring home ranges. Males often combine loud calling with a branch shaking-display (pers. observation) creating additional noise.

These findings support the second hypothesis in the introduction, and indicate that loud calling in this species functions as a ritualized aggressive display of pairs for territory defence. Our observation, that loud calling of one pair may evoke loud calling of pairs in the vicinity, is in accordance with this hypothesis. The fact that loud calling sequences contain sex-specific syllables and carry individual-specific signatures confirms the third hypothesis in the introduction, and implies that this vocal display signals pair ownership to neighbours and strangers, without the necessity of direct, costly fighting.

This is the first empirical evidence in nature that loud calling in the nocturnal Prosimii may act as a mechanism for regulating spacing and cohesion. Ongoing playback experiments will show to what extent sportive lemurs are able to recognize the revealed categories, based on the respective acoustics.

5.4.3 Loud calling between pair partners, and its evolution among primates

In mammals, the presence of loud calling exchanges between both sexes is fairly rare. So far it is described as singing or duetting behaviour solely for primates, e.g., in one diurnal lemur species of Madagascar (*Indri indri*, Pollock 1986), in nocturnal tarsiers of south east Asia (*Tarsius* spp., e.g., MacKinnon and MacKinnon 1980; Wright and Simons 1984;Niemitz 1984; Nietsch 1999), in nocturnal night monkeys (*Aotus* spp.) and in diurnal cebids (*Callicebus* spp.) of Latin America (e.g., Robinson et al. 1987; Müller and Anzenberger 2002; also *Pithecia* spp., e.g., Robinson et al. 1987), in one diurnal southeast Asian leaf monkey (*Presbytis potenziani*, Tilson and Tenaza 1976) and in all species of the southeast Asian small apes (*Hylobates* spp., e.g. Marshall and Marshall 1976; Haimoff 1986; Geissmann 2002).

Our study presents first evidence that antiphonal loud calling of both sexes has also evolved in dispersed pairs of a nocturnal, territorial primate in which it was associated with potentially restricted resources. Despite of divergences in phylogeny, activity pattern and habitat, all of the former primate taxa share four common traits: arboreality, territoriality (exclusive usage of home range), social monogamy and permanent pair cohesiveness. Singing or duetting in them is suggested to strengthen pair bonds (Geissmann, 2002).

The Milne Edwards' sportive lemur has evolved all of these traits, except for permanent pair cohesiveness. This suggests that the elaborated, highly synchronised singing or duetting behaviour in permanently cohesive pairs may originate from antiphonal loud calling in dispersed pairs. Thus, nocturnal lemurs with their broad diversity in social patterns provide unique models both for gaining deeper insight into the evolution of mechanisms regulating spacing and cohesion in male-female groups, and for illuminating the origin and evolution of primate vocal communication.

5.5 Conclusions

An exclusive pair-specific usage of sleeping sites and home ranges, and long-lasting sleeping associations, indicate pair bonding and territoriality in a nocturnal solitary foraging primate, the Milne Edward’s sportive lemur.

Loud calling is a coordinated activity of pair partners, primarily located at potentially restricted resources such as feeding or sleeping sites during dispersals in the evenings and reunions in the mornings. Simultaneous direct agonistic conflicts between pairs and conspecifics are rare. The production of a set of sex- and individual-specific call types in loud call sequences provides the substrate for signalling and the potential for recognizing pair ownership. Thus, our findings imply that the antiphonal loud calling of pair partners functions as a co-operative display of territory defence, regulating spacing and cohesiveness between pairs and neighbours in solitary foraging, pair-bonded primates.

Dispersed, pair living primates may thus provide unique models for illuminating the evolution of sociality and communication in permanently cohesive groups.

6 Study 3

Specific acoustic divergence in communication of cryptic species of nocturnal mammals: social calls and their perception in Malagasy primates (*Microcebus* ssp.)*[3]

A central question in evolutionary ecology is how cryptic species maintain species cohesiveness in an area of sympatry. The coexistence of sympatrically living cryptic species requires the evolution of species-specific signalling and recognition systems. In nocturnal, dispersed living species, specific vocalisations may act as ideal premating isolation mechanisms. We studied male advertisement calls of three nocturnal, dispersed living mouse lemur species, the grey mouse lemur (*Microcebus murinus*), the golden brown mouse lemur (*M. ravelobensis*) and the Goodman's mouse lemur (*M. lehilahytsara*). The first two species occur sympatrically, the latter lives allopatrically to them. A multi-parameter sound analysis revealed prominent differences in the frequency contour and in the duration of advertisement calls. To test whether mouse lemurs respond specifically to calls of the different species, we conducted a playback experiment with *M. murinus* from the field using advertisement calls and alarm whistle calls of the three species. Individuals responded significantly stronger to conspecific than to heterospecific advertisement calls but there were no differences in response behaviour towards statistically similar whistle calls of the three species. Furthermore, sympatric evoked weaker interest than allopatric advertisement calls. Our results indicate a different relevance of particular call types for speciation in nocturnal primates. The evolution of specific differences in signalling and recognition systems on the basis of natural and sexual selection seems to represent an efficient premating isolation mechanism contributing to species cohesiveness in sympatrically living species.

*[3] **dataset *puplished in*:** Braune, P.; Schmidt, S.; Zimmermann, E. (2008) Acoustic divergence in the communication of cryptic species of nocturnal primates (*Microcebus ssp.*) BMC Biol. 6: 19.

Introduction

Cryptic species are closely related species, which are morphologically similar, but differ genetically (e.g. Mayr 1977; Templeton 1998). The recent development in molecular taxonomy and systematics has uncovered a rich diversity of cryptic species, in particular for nocturnal mammals (e.g. Mayer and von Helversen 2001; Pastorini et al. 2001; Olson et al. 2004; Yoder and Yang 2004).

A fundamental problem for sympatrically living, cryptic mammalian species is the coordination of reproduction between conspecifics in time and space, especially when individuals of a species forage solitarily. Under these circumstances mating partners do not only have to detect, localise and find each other, they also have to discriminate conspecifics from remarkably similar looking heterospecifics. Current evolutionary theory (e.g. Mayr 1977; Paterson 1985; Templeton 1989; Andersson 1994) suggests that species cohesiveness in sympatry requires signalling and recognition systems acting as premating isolation mechanisms in order to avoid costly hybridisation. Sexual selection may cause a faster evolution of behavioural than of morphological traits (Jones 1997; Yoder et al. 2002). While this theory has been supported by studies on advertisement calls of crickets (e.g. Higgins and Waugaman 2004; Honda-Sumi 2005), frogs (e.g. Höbel and Gerhardt 2003), songs of birds (e.g. Irwin et al. 2001, de Kort et al. 2002), song repertoires of gerbils (Dempster and Perrin 1994) and social calls of bats (Barlow and Jones 1997), empirical data on other mammalian groups such as primates are still missing.

The Malagasy mouse lemurs, small nocturnal primates which inhabit the fine branch niche of forests, provide an excellent model to explore the significance of vocal communication for species recognition and discrimination. At present 12 cryptic species are known which are difficult to distinguish in body characteristics (Rasoloarison et al. 2000; Yoder et al. 2000; Kappeler et al. 2005; Olivieri et al. submitted). In several areas two species occur sympatrically. Mouse lemurs live in a dispersed social system (cf. Radespiel 2000; Weidt et al. 2004; Schülke and Ostner 2005). During the mating period, vocal activity in mates is enhanced (Zimmermann & Lerch 1993; Buesching et al. 1998), males actively search for oestrous females during the night and female choice may prevail (Craul et al. 2004; Eberle and Kappeler 2004a).

Mouse lemurs have large mobile ears, exhibit a high auditory sensitivity (Niaussat and Petter 1980), are highly vocal and show a rich repertoire of social calls (Zimmermann 1995a; Zietemann 2001). Male advertisement calls of allopatric mouse lemur species (the grey and the Goodman’s mouse lemur) exhibit significant differences in call structure whereas alarm calls do not (Zimmermann et al. 2000). Until now, however, it is neither known whether there are differences in vocal communication between sympatric species nor whether mouse lemurs recognise differences between advertisement calls across species.

We studied the male advertisement calls of the grey, the golden brown and the Goodman's mouse lemur, formerly lumped together with the rufous mouse lemur (*M. rufus*). These three species are genetically distinct from each other (Pastorini et al. 2001), but share a high amount of morphological features (e.g. Zimmermann et al. 1998; Olivieri et al. submitted). The first two species live sympatrically in dry deciduous forest of north-western Madagascar. The Goodman's mouse lemur, on the other hand, inhabits rain forest areas in eastern Madagascar, i.e. it occurs allopatrically to the other studied species.

The present study gives the first account of the relevance of communication calls for species recognition and discrimination in cryptic primates in an area of sympatry. Three questions were raised:

1. To which extent do advertisement calls of sympatric cryptic mouse lemurs differ in structure?
2. Do mouse lemurs discriminate between advertisement calls of different species? Do they show stronger discrimination between conspecific and sympatric than between conspecific and allopatric calls?
3. Do mouse lemurs discriminate between call types of different species which are irrelevant for species recognition in the reproductive context?

6.1 Methods

6.1.1 Recording and analysis of advertisement calls

Male calls were recorded in the presence of oestrous females (c.f. Polenz 2000; Zietemann 2001). Calls of five grey mouse lemurs and four golden brown mouse lemurs from the Ampijoroa population and five Goodman's mouse lemurs from the Hannover laboratory colony (originating from Andasibe, Madagascar) were recorded using two different media: a 1/2" Bruel & Kjaer microphone (type 4133) with preamplifiers (type 2669 and 2619) connected to a NAGRA IV-SJ tape recorder (Kudelski SA, Switzerland) equipped with BASF tapes (ferro LH HiFi TP18, 38 cm/s); or a bat detector (U30, Ultrasound Advice) connected via a filter/control unit (Pettersson) to a high-speed A/D-card (DAS 16/330, Computerboards, Inc.) in a laptop (Compaq Armada) using the recording software BatSoundPro 3.0. All advertisement calls were recorded from caged animals at a distance of about 1 m. The vocalisations recorded with the

NAGRA tape recorder were replayed with half speed and digitised with a sampling rate of 44.1 kHz (16 bit).

We analysed all calls with BatSoundPro 3.0, using a FFT size of 512 and a Hanning window for spectrograms. For each advertisement call, we measured its duration (dur), minimum ($f_0$min) and maximum ($f_0$max) frequency of the fundamental and calculated the bandwidth of the fundamental ($f_0$band = $f_0$max - $f_0$min). Per individual, we analysed three to 21 (median = 5) calls and calculated individual median values for each acoustic parameter. On the basis of these values we conducted a Kruskal-Wallis ANOVA to test for species-specificity. Statistics were made using Statistica 6.0 (StatSoft Inc.), the level of significance was 0.05 for all statistical tests.

6.1.2 Playback experiments

Playback experiments were conducted in the Ankarafantsika National Park (16°19´S, 46°48´E), about 110 km south-east of Mahajanga, Madagascar during the dry season from September to October 2000 and from July to October 2001 covering the mating period of the mouse lemurs. They were performed in a part of the dry deciduous forest where the grey and the golden brown mouse lemur occur sympatrically.

16 (13 males, 3 females) grey mouse lemurs were subjects of our playback experiments. The experiments were conducted under temporary captivity conditions in the field. A stationary setup under controlled conditions was necessary because mouse lemurs communicate in the ultrasonic range which requires a special playback and recording equipment. To test for differences in the perception of sympatric and allopatric calls, we needed animals from the field which were experienced with their sympatric species.

The intervention on the individual and population level by the experimental study was reduced to a minimum by the following procedure: we trapped the animals using Sherman Live Traps (HB Sherman Traps, Inc., Tallahassee, Florida) by setting them in the late afternoon in trees and bushes (Zimmermann et al. 1998). Traps were equipped with pieces of banana providing sufficient food and water supply for a night. Mouse lemurs have adaptations to dry conditions as they are able to gain water by metabolising brown fat tissue (Génin et al. 2003). Traps were checked and collected in the early mornings.

Captured mouse lemurs were brought to the observation cages in their traps. Individually identified animals were placed singly in cages of 1.2 m x 1 m x 0.5 m installed between bushy vegetation. These observation cages were equipped with a bamboo trunk as a nesting place, several branches and a bowl filled with water. The animals were fed with pieces of banana daily and they caught insects, which entered the cages. The animals were housed between three and five nights and released afterwards at their capture point at sunset. Different caging time was due to a different habituation time individuals needed to move normally in the presence of an observer and the number of playback sessions in which they performed (cf. below). No individual which took part in the experiments showed any abnormal behaviour or injuries while housed in the cage. All mouse lemurs ate normally, moved in the cage and showed a normal day-night rhythm. Due to the fact that mouse lemurs are seasonal breeders (Schmelting et al. 2000), it was guaranteed that no female was lactating or even advanced in pregnancy.

After their release, many of the tested mouse lemurs were trapped again in their previous home range: some after several days, others also in the following year, i.e. the location of trapping was not avoided and trapping had no negative consequences for the individuals. In addition, former studies showed that trapping as applied in our study had no adverse effects on mortality or other aspects of behaviour (Radespiel 1998; Schmelting 2000) and did not have a lasting effect on the population structure of grey mouse lemurs in our study area (Radespiel et al. 2001a, 2003b; Lutermann et al. 2006; Mester 2006).

Six categories of playback stimuli were presented: conspecific male advertisement calls (referred to as conspecific advertisement), heterospecific male advertisement calls of the golden brown mouse lemur (referred to as sympatric advertisement), heterospecific male advertisement calls of the Goodman’s mouse lemur (referred to as allopatric advertisement) and male whistle alarm calls (Zimmermann 1995a; Scheumann et al. in press) of all three species (referred to as conspecific whistle, sympatric whistle and allopatric whistle, respectively).

A playback stimulus consisted of one call for the categories conspecific and sympatric advertisement, two calls for the category allopatric advertisement and three calls for the three whistle categories, respectively. By this setup we accounted for the different duration and repetition rates of male advertisement calls and short whistles from the different species. We used two different advertisement stimuli from each of four conspecific males and two different stimuli from each of two sympatric and allopatric males. As whistle stimuli, we used two short whistles each of two males of the grey, two males of the golden brown and one male of the Goodman’s mouse lemur.

With these stimuli, we produced four playback tapes, each including two different stimuli of the category conspecific advertisement and one stimulus of all other call categories, resulting in a total number of seven different stimuli in a random order. To minimise background noise the stimuli were highpass filtered at a frequency of 7 – 15 kHz depending on the minimum frequency of the call. The playback of a tape was started at a random position using a NAGRA

IV-SJ tape recorder (Kudelski SA, Switzerland), a custom-made amplifier and a speaker (Leaf Tweeter EAS-10Th400A).

Stimuli ranged between 70.5 and 83.0 dB SPL at a distance of 1 m (RMS, Bruel & Kjaer Measuring Amplifier Type 2610), i.e. sound pressure levels corresponded to the naturally occurring ranges. The loudspeaker was placed 0.6 – 0.8 m above ground at a distance of about 0.5 m from the cage to ensure a good presentation of the highly directional ultrasonic calls at any position in the cage. To avoid a habituation to playback stimuli, the inter-stimulus interval was kept between one and ten minutes. Each individual took part in one to three playback sessions in which a full tape was played back.

Behavioural responses to playback stimuli were observed at a distance of about 5 m from the observation cage using a head lamp and a binocular and reported to a dictaphone for further analysis. We recorded the behavioural responses within 10 seconds just after the onset of a stimulus. In all cases, response behaviour had finished within this period. Responses were classified into two different response categories: 1. no orientation, not involving any orientation response including no reaction, ear movement, interruption of activity or startle without turning towards the speaker and 2. orientation, including turning towards the speaker and approaching the speaker, sometimes accompanied by antiphonal vocalisation.

Cases were excluded in which animals were not visible to the observer because they went into their bamboo trunk or were hidden by cage enrichment. 186 responses to playback stimuli could be analysed. The frequencies of no orientation and orientation responses were determined per stimulus and per individual, respectively. We recorded five to 13 (median = 8) responses for each stimulus. Each individual contributed between three and 20 responses (median = 11.5). The behavioural responses were counted for the respective response categories and visualised within each call category.

We conducted Spearman rank correlations to exclude effects of stimulus quality by correlating the response indices of the stimuli with their sound pressure level and their signal to noise ratio, respectively. A stimulus response index was defined by the number of orientation responses divided by all responses towards a stimulus. To make sure that the consecutive presentation of playback stimuli resulted in independent responses we conducted a Spearman rank correlation for the response indices with the order of stimulus presentation. The order response index was defined by the order number of the orientation responses divided by all responses for the respective presentation number. Furthermore, to test for habituation effects we analysed if the response strength towards the first and the second stimulus of that class differed significantly for the two conspecific advertisement stimuli during a given playback session (Chi-square test).

For statistical comparison of call categories, an individual-based analysis was conducted comparing individual response indices for all call categories of advertisement calls and short whistles, respectively. The individual response index towards a call category was defined by the number of orientation responses divided by all responses of an individual towards stimuli of the respective call category. A Friedman-ANOVA and Wilcoxon-tests with a serial Bonferroni correction procedure (cf. Engel 1997) were performed for each call type.

6.2 Results

6.2.1 Interspecific comparison of advertisement calls

The frequency contour of the harmonically structured advertisement calls from the three species was remarkably different (Fig. 6-1). The grey mouse lemur produced an acoustically complex frequency modulated advertisement call with an upward frequency modulated sweep followed by a tail containing several sinusoidal modulations. The advertisement calls of the golden brown mouse lemur consisted of two to six generally upward frequency modulated components. Occasionally, a component contained a nearly constant frequency part and / or ended with a downward frequency modulated hook. The Goodman’s mouse lemur emitted a two-component call of relatively stereotypic structure with an upward followed by a downward modulated element separated by a short inter-element interval.

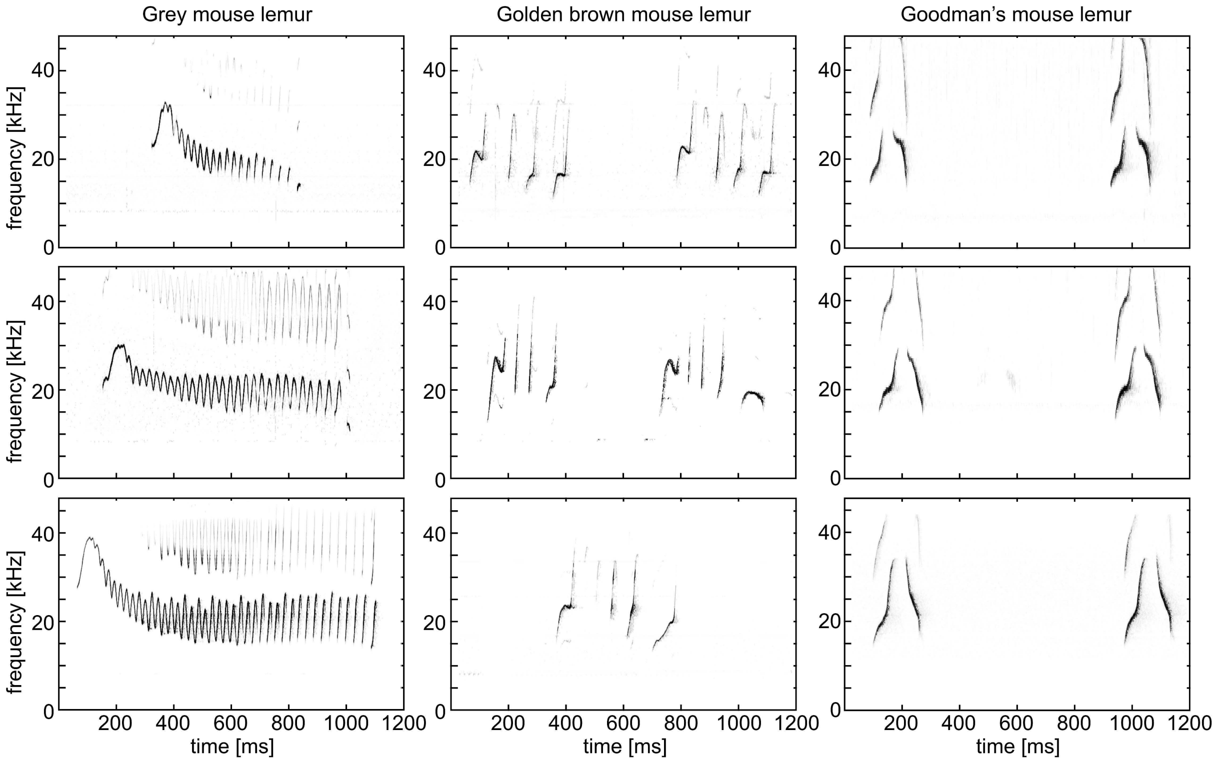

Fig. 6-1: Representative sonagrams of advertisement calls emitted by three different individuals of the three studied mouse lemur species.

No measured frequency parameter showed any species specificity (Kruskal-Wallis test: $f_0$min: $H_2 = 3.470$, $p = 0.176$, $f_0$max: $H_2 = 0.928$, $p = 0.629$, $f_0$band: $H_2 = 2.566$, $p = 0.278$, $N = 14$ for all tests; Table 6-1), i.e. the absolute frequency ranges and the bandwidths of the advertisement calls of the three species were comparable. Call duration, however, differed significantly between the three species (Kruskal-Wallis test: $H_2 = 11.623$, $p = 0.003$, $N = 14$). The calls of the grey mouse lemurs were the longest, those of the Goodman's mouse lemur the shortest and those of the golden brown mouse lemur took an intermediate position.

Table 6-1: Comparison of advertisement calls of three mouse lemur species[7].

species	acoustic parameter	median	minimum	maximum	25th percentile	75th percentile
M. murinus **(N=5; n=30)**	dur [ms]	870	710	1040	870	985
	$f_0$min [kHz]	12,30	12,00	13,95	12,20	13,80
	$f_0$max [kHz]	35,90	34,90	37,80	35,60	36,40
	$f_0$band [kHz]	23,10	20,90	25,20	21,60	23,20
M. ravelobensis **(N=4; n=39)**	dur [ms]	375	360	430	365	405
	$f_0$min [kHz]	12,50	11,60	13,35	11,65	13,33
	$f_0$max [kHz]	37,00	33,00	38,70	34,70	38,15
	$f_0$band [kHz]	24,13	21,60	26,70	22,70	25,58
M. lehilahytsara **(N=5; n=20)**	dur [ms]	135	120	160	135	150
	$f_0$min [kHz]	13,8	12,50	15,75	12,85	14,75
	$f_0$max [kHz]	34,5	27,55	40,70	30,75	37,5
	$f_0$band [kHz]	19,8	14,70	26,90	18,25	21,75

[7]: N=number of individuals; n=number of calls; for abbreviations see Methods: Recordings and analysis of advertisement calls

6.2.2 Behavioural responses to advertisement and short whistle stimuli

In the 186 analysed responses the animals showed an orientation response in 101 cases, including 85 times turning towards the speaker and 16 times approaching the speaker. In one of the latter cases for one time a male additionally uttered an advertisement call after the presentation of a conspecific advertisement call. In the remaining 85 cases the animals showed no reaction to the stimuli in 48 cases, ear movement in 14, interruption of activity in 12 and startle without turning towards the speaker in 11 cases. An overview about the distribution of no orientation and orientation responses within the six call categories is given in Figure 6-2.

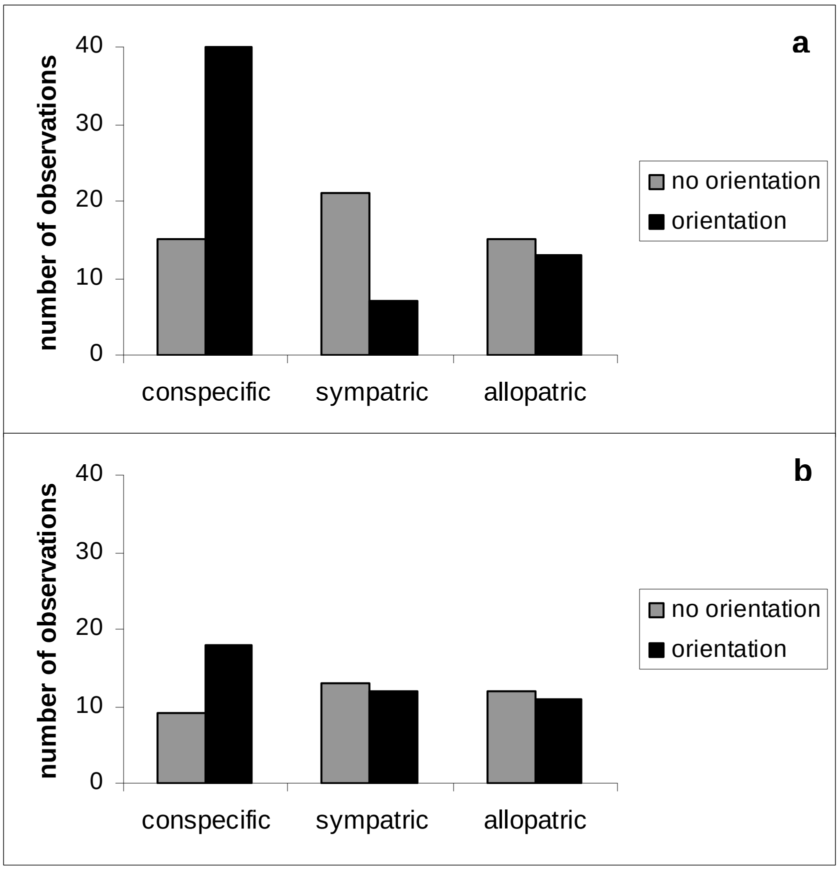

Fig. 6-2: Responses of grey mouse lemurs to playbacks of conspecific (=*M. murinus*), sympatric (=*M. ravelobensis*) and allopatric (=*M. lehilahytsara*) advertisement call stimuli and short whistle stimuli.

Neither the sound pressure level nor the signal to noise ratio of stimuli had significant effect on the stimulus response indices (Spearman rank correlations: sound pressure level: $r_S = 0.068$, $N = 22$, $P > 0.05$; signal to noise ratio: $r_S = 0.411$, $N = 22$, $P > 0.05$). In addition, response strength was independent of the presentation number of stimuli (Spearman rank correlation: $r_S=0.088$, $N=12$, $P>0.05$). This shows that inter-stimulus intervals were sufficient to avoid any habituation effects due to the consecutive stimulus presentation design. The distribution of no orientation and orientation responses did not differ significantly between the first and the second conspecific advertisement stimulus presented in a given playback tape (Chi-square-test: $\chi^2= 0.149$, $P=0.7$). Therefore, all responses towards conspecific advertisement stimuli were lumped together for further analysis.

Individual response indices revealed remarkable differences for conspecific, sympatric and allopatric stimuli (ANOVA $\chi^2_2 = 12.298$, $P < 0.002$; $N = 15$; Fig. 6-3). Thus, individuals reacted significantly more frequently with orientation responses towards conspecific than towards both sympatric and allopatric advertisement stimuli. This suggests a high interest of grey mouse lemurs for conspecifics advertisement stimuli compared to heterospecific advertisement stimuli.

Furthermore they responded significantly more frequently with orientation responses towards allopatric than towards sympatric advertisement stimuli (Wilcoxon signed-rank tests: conspecific – sympatric: T = 4.0, N = 15, P = 0.004; conspecific – allopatric: T = 15.0, N = 16, P = 0.033; sympatric – allopatric: T = 4.0, N = 15, P = 0.05; the conspecific – sympatric and sympatric – allopatric comparisons remained significant after serial Bonferroni-correction).

In contrast, the individual-based analysis showed no significant differences in response strength towards all short whistle categories (ANOVA $\chi^2_2 = 0.780$, N = 12, p < 0.677; Wilcoxon signed-rank tests: conspecific – sympatric: T = 25.5, N = 13, P = 0.29; conspecific – allopatric: T = 15.0, N = 12, P = 0.374; sympatric – allopatric: T = 26.0, N = 13, P = 0.878; Fig. 6-3). These findings suggest that the grey mouse lemurs had no preference for any category of the short whistles.

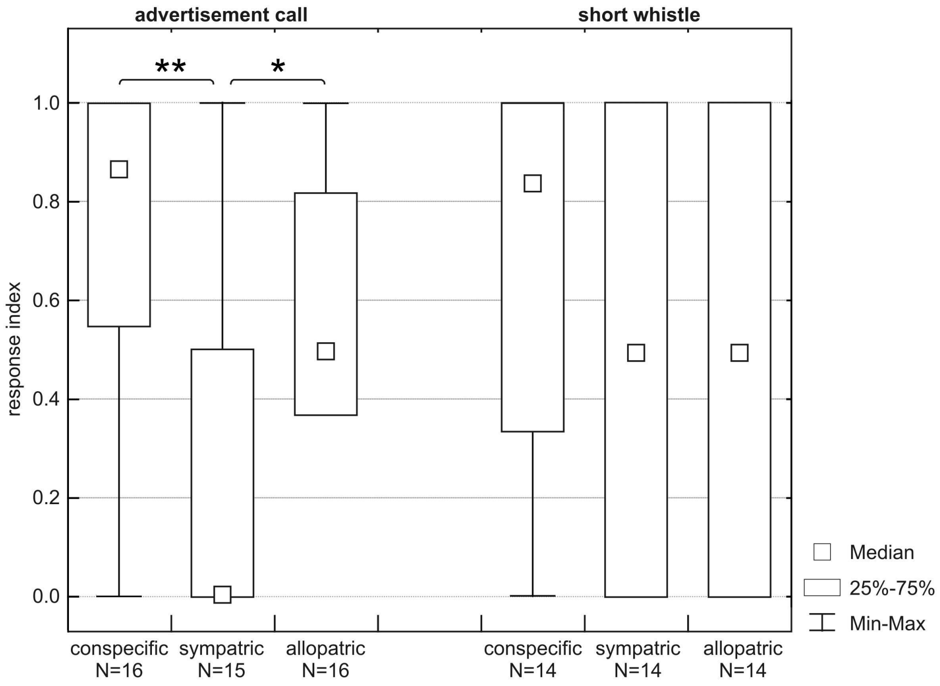

Fig. 6-3: Individual response indices for the different call categories. N= number of individuals, * indicate significant differences after serial Bonferroni correction (* p<0.05, ** p<0.01).

6.3 Discussion

The interspecific comparison of male advertisement calls of three mouse lemur species revealed structural differences as well as differences in response behaviour to playbacks. Both indicate a species-specific function of these calls. Conspecific calls evoked the strongest responses. Playback experiments furthermore suggest a different relevance of heterospecific advertisement calls with regard to sympatry or allopatry as sympatric calls evoked lower responses than allopatric calls. In contrast, no preference for any whistle call category was found.

6.3.1 Species-specific structure in advertisement calls

The evolution of species-specific signals is driven by a trade-off between sensory system characteristics, predation, environment and mate choice criteria (Endler 1992). In the present study, all species used broadband, frequency modulated advertisement calls in the same frequency range. Broadband, frequency modulated signals provide advantages for sound localisation (Wiley and Richards 1982; Brown and May 1990). Uniformity in frequency range may be explained by similar morphological constraints (e.g. Hauser 1993) and similar predation pressure (Marler 1955) for the three species studied.

On the other hand, we found species-specific frequency contours in the advertisement calls which play an important role in courtship and mating of mouse lemurs (cf. Buesching et al. 1998; Craul et al. 2004). This divergence may reflect the high sexual selection pressure existing for advertisement calls (Ryan and Kime 2003). Moreover it constitutes first evidence in primates for a behavioural trait evolving faster than morphological traits. The species-specific differences of advertisement calls could have evolved as an adaptation to transmission over long distances in different microhabitats as suggested for a number of different vertebrate taxa (e.g. Ryan et al. 1990; Brown et al. 1995; Kopuchian et al. 2004). According to this habitat adaptation hypothesis (Morton 1975), longer calls with short, rapidly repeated elements are favoured in more open habitats and shorter, slower modulated elements in denser vegetation structure (Wiley and Richards 1978).

In fact, the grey mouse lemur lives in dry deciduous forests and produces the longest call consisting of partially connected, rapidly repeated short elements. In contrast, the Goodman’s mouse lemur, which occurs in rain forest areas characterised by dense vegetation emits the shortest call consisting of two longer elements only. Accordingly, shorter calls with separate, slower modulated elements might have been the primary adaptation to the rain forest habitat. The call of the golden brown mouse lemur, which lives sympatrically with the grey mouse lemur, but is genetically closer related to the Goodman’s mouse lemur (Pastorini et al. 2001) takes an intermediary position. An immigration of the golden brown mouse lemur from rain forests into more open habitats (cf. Martin 1995; Ganzhorn and Schmidt 1998; Godfrey et al. 1999) may have driven selection towards longer calls with separate, relatively slowly modulated elements. Thus, our results support the habitat adaptation hypothesis.

6.3.2 Species-specific call recognition

Structural differences in advertisement calls of the three species do not necessarily represent evidence for the use of these calls in conspecific recognition. We showed in this study that grey mouse lemurs responded similar towards the structurally similar whistle calls of the three species. This is not surprising as they occur in alarm situations (Scheumann et al. in press) for which calls of a similar structure are used by a broad range of species and yield to the same anti-predator responses (Marler 1955). As these calls are not counter selected by sexual selection this trait remains stable.

In contrast, species-specific recognition of advertisement calls plays an important role for reproduction in cryptic and dispersed living species where females and males have to find each other for courtship and mating (Jones 1997). Thus, a positive response behaviour towards heterospecific calls would have a negative impact on the fitness of individuals as they would risk costly hybridisation. These aspects should be more relevant for sympatric than for allopatric species. Our playback experiment confirms the above hypothesis for the first time in dispersed living primates: conspecific calls caused stronger interest than heterospecific calls. This response behaviour was not due to differences in stimulus quality. Therefore, an influence of sound quality on the response behaviour does not account for the differential responses to the different stimulus classes.

We found more pronounced differences in the perception of conspecific versus sympatric than versus allopatric calls. Comparable differences in perception have been reported from a wide range of species (e.g. Gwynne and Morris 1986; de Kort and ten Cate 2001; Höbel and Gerhardt 2003; Honda-Sumi 2005). Character displacement (Brown and Wilson 1956; Howard 1993) as a result of selection against hybrids may cause species-specificity in recognition systems (cf. Höbel and Gerhardt 2003 for frogs). This explanation may also account for our data (see however Irwin 2000 for birds). Alternatively, the observed differences in the perception of sympatric and allopatric advertisement calls could be a result of different exposure of the grey mouse lemurs to these calls. The grey mouse lemurs in our experiments were long-term habituated to the sympatric calls and the increased attention towards the allopatric calls compared to the sympatric calls may represent a novelty-effect (cf. Tulving and Kroll 1995). To sum up, this study provides first evidence for specific acoustic divergence in communication of cryptic species of nocturnal mammals living in sympatry, which is a prerequisite for species cohesiveness.

7 General discussion

The inter- and intra-specific acoustic variability is influenced by several species- and individually-dependent factors resulting in a variety of evolutionary selection pressures on signal structure, occurrence and function. In this thesis the impact of some factors were analysed, whereas, others were kept the same using mouse and sportive lemurs living in the same ecological community in the Malagasy forests as models.

7.1 Factors influencing the acoustic variability on the inter-and intra-species level

In the following chapter I will apply a model to explain the results of the presented studies (chapter 4-6). This model will integrate several factors that can have an impact on the inter- and intra-specific acoustic variability (Fig. 7-1). The results of the presented studies will be reviewed and discussed in the light of factors that have been relevant for this thesis.

In general, factors influencing the *inter-specific* acoustic variability represent those which can differ between species. Although these may also have repercussions for *intra-specific* communication concerns, this aspect mainly relies on differences distinguishing the individuals or individual associations as sleeping groups or populations within a species from one another.

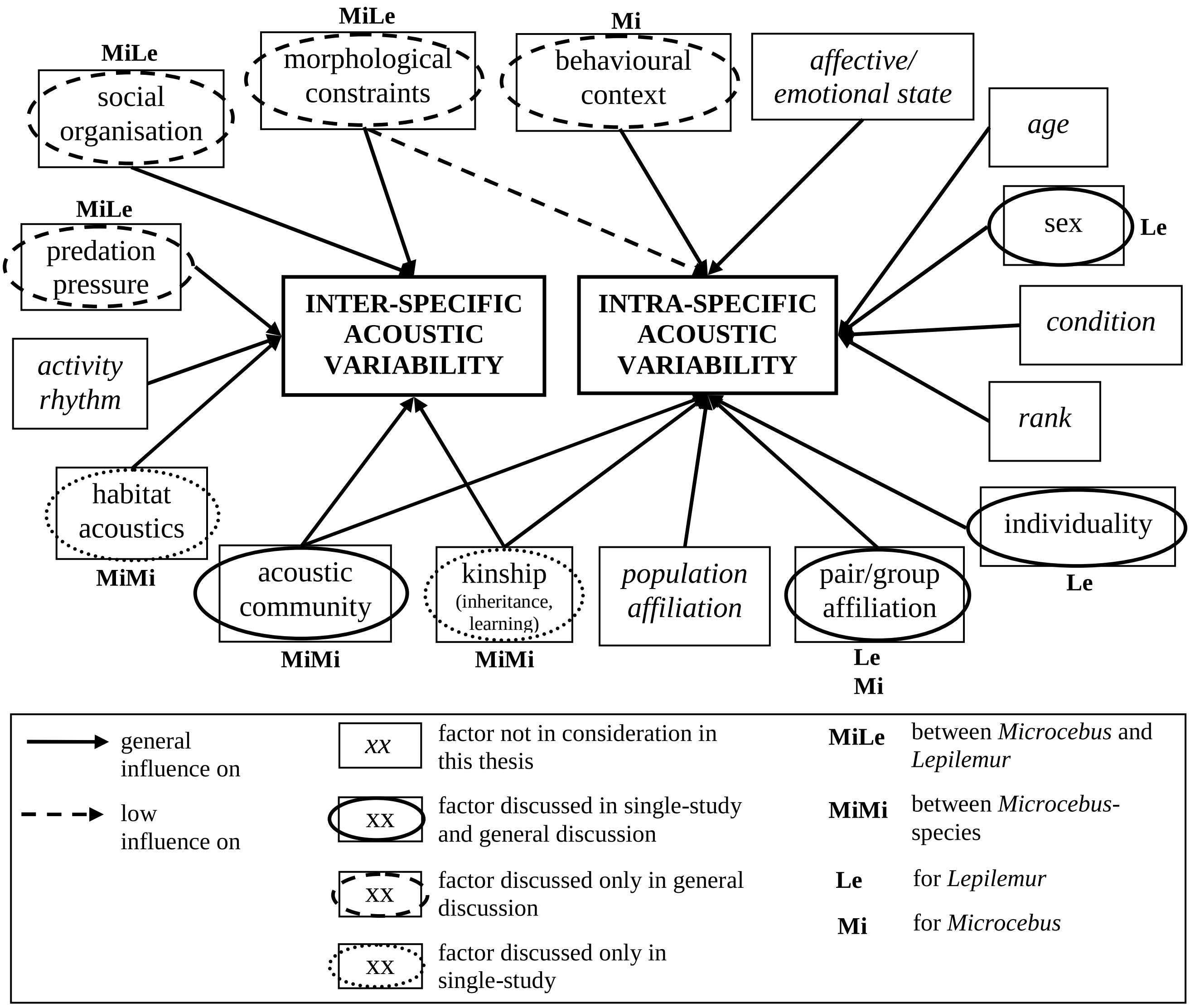

Fig. 7-1: Examples of factors influencing inter- and intra-specific acoustic variability for communication between and within species. Several factors influence one another and may indicate new connections. However, these have been omitted due to clarity in the presentation of the figure. Important aspects deriving from these additional connections will be annotated in the discussion of the respective factors.

7.1.1 Inter-specific acoustic variability

Important factors suggesting an influence on inter-specific acoustic variability are ***habitat acoustics***. For species occurring in different habitats the structure of their calls would be adapted to the environmental conditions through natural selection in order to optimise transmission of their acoustic signals (e.g. Gish and Morton 1981; Wiley and Richards 1982; Brown and Waser 1988). Furthermore, also the occurrence and function of calls may depend on habitat parameters: forest-living species are expected to code the respective context more obviously in signal structure because in most cases they are not able to combine the acoustic signal with additional visual ones (e.g. Snowdon et al. 1983). Thus, forest species may show higher call variability than for example savannah-living species due to a high importance of precise and variable information transfer between conspecifics through the acoustic channel.

This aspect should also be relevant with regard to the ***activity rhythm*** of a species. Nocturnal animals can only rely on limited visual abilities, whereas, cathemeral and diurnal species may use multimodal signalling effectively (e.g. Marler 1965; Partan and Marler 1999).

Predation pressure was suggested to be one of the most important selective pressures on free-ranging animals (Treves 2000). Therefore, a different quality and / or quantity of predators could be expected to be an important factor with regard to animal communication signals (cf. Endler 1992). In particular alarm calls of several primate species showed prominent differences in structure and function with respect to social structure and the kind of the predators (e.g. Zimmermann 1985a, b; Macedonia 1990; Goodman et al. 1993; Blumstein and Armitage 1997) indicating the importance of predation pressure on inter-specific call variability (this thesis: chapter 7.4).

Another factor influencing acoustic communication patterns is the ***social organisation*** of the respective species. Generally, the intra-specific call variability is expected to be higher in group- than in solitary living species (see chapter 3.2). Animals which are living in a group, have to overcome a lot of inter-individual concerns including dominance hierarchies, group movement, group cohesion, predator avoidance and food sharing. Furthermore, group members have to manage inter-group concerns, for example the spacing between groups or the switching of group members to another group, depending on the respective social organisation.

For many of these aspects acoustic signals provide valuable tools as has been shown in a variety of primate species already (e.g. group cohesion and movement: (Boinski and Garber 2000). On the other hand, the individuals of solitary living species often rely on crypsis and inter-individual contact is rare. Therefore, the variability of communication signals such as vocalisations should be comparably low. Thus, the intra-specific call variability depends on the social organisation of species and should be drawn on for inter-specific call variability comparison (this thesis: chapter 7.4.1).

7.1.2 Inter- and intra-specific acoustic variability

Morphological constraints may influence both the inter- as well as the intra-specific acoustic variability. The production of sounds depends on morphological parameters: it was generally assumed that a larger body size results in a lower fundamental frequency (F_0) (e.g. Morton 1977, Morton 1982; Gouzoules and Gouzoules 1990) because larger vocal folds being able to produce lower frequencies. Additionally, it was shown that the length of the vocal tract correlates with body size, providing, via formant frequency dispersion, an honest indicator of size (Fitch 1997). Hauser (1993) proved that the vocal pitch in large species is lower than in smaller species, supporting the assumption that vocal pitch represents a reliable indicator of body size on the *inter-species level* of non-human primates (Fitch and Hauser 1995; this thesis: chapter 7.4).

On the contrary, this honest cue was hardly found for the *intra-species level* (e.g. frogs: Wilczynski et al. 1993; Gerhardt 1982; humans: Lass and Brown 1978; Künzel 1989). This may be due to the fact that although the maximum length of the vocal tract may be constrained by skeletal features, it is adjustable via retraction or protrusion of the lips and by raising or lowering of the larynx (Fitch and Hauser 1995).

Thus, the signaller can actively attempt to project a larger or smaller body size dependent on the specific context and function of the call: for example, a larger one in aggressive situations or during mating and a smaller one in appeasement situations. This offers the individuals a broad range of context-dependent call modulation abilities (see below: behavioural context). Body size is of paramount importance in vertebrates, influencing competitive and mating success (Darwin 1871; Wiley 1974; Brown and Maurer 1986). Vocalisations may therefore act as an indicator of individual fitness and may influence the behaviour of a competitor or potential mate towards the signaller.

Several studies suggest that receivers do indeed use pitch as a cue to body size: for example a widespread occurrence of low-pitched growls during aggressive interactions was revealed (Morton 1977, 1982; Hauser 1993). This shows that at least the image of morphological constraints could play an important role in intra-specific acoustic communication involved in fitness display between conspecifics.

Kinship may also influence the acoustic variability on both levels. Species as well as individuals or individual associations can be more or less similar in their acoustic repertoire, its usage and characteristics being due to their phylogenetic relationship. Similarities in the acoustic variability of related individuals may stem from inheritance (e.g. Geissmann 1984) or social learning (e.g. Egnor and Hauser 2004) of specific parameters (see also discussion chapter 1). Kinship aspects were not part of this thesis but current genetic studies on golden brown mouse (M. Juric as well as on Milne Edwards' sportive lemurs (M. G. Mendez Cardenas will offer further valuable information on this subject.

A further aspect which may influence acoustic variability is the occurrence of other related species in the same ***acoustic community***. (Marler 1965) commented: "When animals are communicating under natural conditions there is always a danger that alien sounds will intrude into the system and cause confusion”. He concluded that many vocalisations are specifically distinct.

Indeed, a variety of studies have revealed species-specific calls in a large amount of species, especially in those that communicate largely by acoustic signals including bats, anurans, and many insects and birds (cf. Jones 1997). Especially the sympatric occurrence of sibling or even cryptic species may have an important impact on call structure due to a possible limitation in the recognition of conspecifics on the basis of visual cues because of their morphological similarities (see also chapter 3.2). The impact of sympatry or allopatry can be important not only on the inter-species level as shown in the case of three mouse lemur species (chapter 6), but also on the intra-specific level between different populations of a species living in sympatry or allopatry with another species, respectively, in terms of reproductive character displacement (this thesis: chapter 7.2.1).

7.1.3 Intra-specific acoustic variability

Factors besides morphological constraints (see above) that might influence the acoustic variability of the individual and therefore the intra-specific variability are the individuals’ ***age*** (e.g. Inoue 1988; Hammerschmidt et al. 1994), ***sex*** (e.g. Green 1981; Mitani and Gros-Louis 1995; this thesis: chapter 7.2) or ***condition*** (cf. Andersson 1994). In non-gregarious species this information may be interpreted by potential mating partners and may increase fitness by following appropriate mating strategies (e.g. Alcock 1998; Bailey 1991). Thus, sexual selection on call parameters enhances diversity within species (Ryan and Kime 2003) and advertisement calls may not only lead to individuals of the own species but also to a subset within the species (e.g. Andersson 1994).

In social-bonded species with more complex social systems such calls may be additionally or solely used for individual recognition through call ***individuality*** (e.g. Marler and Hobbett 1975; Hammerschmidt and Todt 1995; Zimmermann and Lerch 1993; this thesis: chapter 2). Furthermore, individual calls may even contain information about the dominance ***rank*** (e.g. Aich et al. 1987; Kitchen et al. 2003b) or the ***affective / emotional state*** (e.g. Morton 1977; Jürgens 1979; Scherer 1992) of the sender. All these aspects may have an influence on call characteristics, the utterance and / or the function of acoustic signals.

The ***behavioural context*** may also have a strong influence on the intra-specific acoustic variability. Intra-specific variation concerning this factor was shown for a variety of non-human primates (e.g. Aich et al. 1990; Zimmermann 1985a, b; Seyfarth et al. 1980; Gouzoules et al. 1984; Zuberbühler et al. 1997; Hohmann and Vogl 1991; Fischer 1998; Kitchen et al. 2003a;

Scheumann et al. submitted). Individuals of a species may adopt a specific call type for a context in slightly varying specific call parameters (this thesis: chapter 7.2), which was in fact shown to be recognised by conspecifics. Of course, this factor is strongly coupled with the factor social organisation of a species as different social systems may have acquired different behavioural contexts (see 3.1.1).

Furthermore, intra-specific acoustic variability may be influenced by the ***population affiliation*** of individuals due to the fact that populations of a species may evolve different call characteristics (e.g. anurans: Ryan and Wilczynski 1988; birds: Krebs and Kroodsma 1980; primates: Maeda and Masataka 1987; Hafen et al. 1998). This may be due to the development of dialects (according to Tembrock 1996) or simply through an adaptation of calls on varying external factors as habitat characteristics, sympatry with other species, predation pressure etc. (cf. Nottebohm 1969; Mundinger 1982).

Within a population ***pair or group affiliation***, respectively, may have an effect on the intra-specific acoustic variability if specific calls show pair- or group-specific call signatures. Those call signatures may be important for spacing between groups and cohesion between group members (see chapter 4+5). Especially in the case when group signatures result from call convergence of unrelated individuals. Take for example greater spear-nosed bats (Boughman 1997) or birds (Mammen and Nowicki 1981; Nowicki 1989) where this factor is important and differs from the factor kinship as group specific call parameters may also be an effect of group member relatedness (e.g. Ford 1989); discussed in this thesis: chapter 7.2).

In this thesis the aspect of *inter-specific acoustic variability* will be discussed on the basis of three species of cryptic mouse lemurs, focussing on the impact of the ***acoustic community*** in the light of sympatric and allopatric living species (chapter 7.3.1). I will be referring to the results of the playback study presented in chapter 6 and the discussion therein concerning the factors ***habitat acoustics*** and ***kinship*** for the different mouse lemur species.

Aditionally, I will provide a comparison between the Milne Edwards’ sportive lemur and the two sympartically living mouse lemur species (chapter 7.4). Here, the two factors activity rhythm and habitat acoustics were the same for the study species due to their shared ecological community in our study area. Under these circumstances I will compare the acoustic variability in mouse lemurs to that of sportive lemurs on the inter-species level concerning the factors ***morphological constraints***, ***predation pressure*** and ***social organisation*** of the different lemur species in view of the findings presented in chapter 4+5.

The *intra-specific acoustic variability* at an ***individual***, ***sex***, ***pair and group level*** for golden brown mouse and Milne Edwards' sportive lemurs, respectively will be discussed (chapter 7.2), referring to the analyses presented in chapter 4+5. Due to the fact that the intra-specific variability of both species represents the basis for the inter-specific comparison, I will begin the discussion with this aspect.

7.2 Intra-specific acoustic variability in mouse and sportive lemurs

The complex structure of species-specific mouse lemur advertisement calls and of sportive lemur loud calls offers a variety of possibilities for signal modulation.

Individuality in call signatures has been shown for a variety of primate species (e.g. Haimoff and Gittins 1985; Chapman and Weary 1990; Hammerschmidt and Todt 1995) and several playback studies have even revealed their biological significance (e.g. Cheney and Seyfarth 1982; Symmes and Biben 1985; Rendall et al. 1996). The advertisement of those signatures by way of acoustic signals may facilitate or even allow the evolution of group living societies, providing the potential for the management of complex social networks. Interestingly, individual call signatures have been shown even for the ancestral primate forms as nocturnal lemurs: also male mating advertisement calls of mouse lemurs (Zimmermann and Lerch 1993; Hafen 1998; Polenz 2000) and several loud calls of the Milne Edwards' sportive lemurs (chapter 5) carry individual-specific signatures. This may indicate that even in such ancestral forms of gregarious living, the organisation being in dispersed pairs or groups, may profit from individual discrimination and recognition.

One factor that may influence individual signatures but, which could also be interpreted as an independent factor is **sex** difference. This factor may be crucial for animals such as primates that must navigate complex social systems (e.g. Egnor et al. 2005). As an example cotton top tamarins utter species-specific long calls when separated from their group and elicit antiphonal calls and approach behaviour from conspecifics (Miller et al. 2004). Their calls are sex-specific regarding syllable duration and are preferred by the opposite sex. Data in this thesis showed, that in Milne Edwards' sportive lemurs, the discrimination between the sexes is predominantly given by the use of different call types. The one exception, the high pitched call (HPC), also showed sex-specific call duration and can therefore be differentiated by the individuals.

In the case of mouse lemurs no research on sex-specific signatures in advertisement calls has been carried out so far. As already ascertained by (Masters 1991) high quality recordings of nocturnal solitary ranging forest living primates that can be assigned to the respective sender and its behaviour are difficult to record. Unfortunately, in the presented study on free-ranging golden-brown mouse lemurs (chapter 4) assigning of recorded calls to a specific individual of a dispersing or reuniting sleeping group was impossible in most cases as well. Due to the fact that grey and Goodmans' mouse lemurs show advertisement calling behaviour even in the laboratory this aspect could be an interesting topic for a future laboratory study.

Apart from individual recognition, group living animals may rely on group-specific signatures in their communication signals coding for a specific ***group affiliation*** (e.g. Biben 1994). Especially species organised in dispersed living groups in which the group members have to re-aggregate regularly, or species in which the spacing of groups plays an important role, could profit from group signatures. These could originate from a genetic determination of call signatures in closely related family groups or may result from an adaptation of call structures with respect to locality or group-membership (e.g. birds: Nowicki 1989; Hopp et al. 2001; dolphins: Fripp et al. 2005; bats: Boughman 1997). First genetic data indicate various degrees of relationship between golden-brown mouse lemur sleeping group members (Juric pers. comm.). Thus, both explanations could explain the group-specificity of gathering calls.

In order to clarify these aspects, further studies of individually marked animals are necessary including genetic and acoustic analyses. Nevertheless, golden-brown mouse lemurs as well as Milne Edwards' sportive lemurs may recognise their sleeping partners and discriminate them from conspecifics of other sleeping groups due to acoustic signatures in their long distance calls used during dispersal and reunion of groups. Intra-specific variation of their calls on the basis of individuals and / or groups may thus facilitate or even allow these nocturnal lemurs to live gregariously at least temporarily.

Intra-specific variation of a call type dependent on a specific ***behavioural context*** was come across in a variety of non-human primates (e.g. Seyfarth et al. 1980; Gouzoules et al. 1984; Hohmann and Vogl 1991; Zuberbühler et al. 1997; Fischer 1998; Fischer and Hammerschmidt 2001). For example, tamarin long calls revealed that these calls served two different functions and that call structure varied depending on function (Moody and Menzel 1976; Snowdon et al. 1983). When the call served for inter-group and distance communication it was uttered in a long and loud version. However, when this call was used for inter-group cohesion and as a rallying call it was emitted in a shorter and softer version.

This thesis revealed for golden brown mouse lemurs (and unpublished data for grey and Goodmans' mouse lemurs as well) a usage of comparable species-specific advertisement calls in two different contexts: during courtship (mating calls) and during group re-aggregation (gathering calls). A structural and perceptual comparison of advertisement calls uttered in these two different contexts is lacking so far. However, a laboratory study on grey mouse lemurs revealed significant differences in advertisement call structures of males emitted during mating activities in the presence of a female (mating calls) compared to those emitted during fights with another male, indicating yet a further context in which this call type is used (Dietz 2006). This shows the ability to adapt an advertisement call structure depending on the respective context. Therefore, it would appear that a structural comparison of mating and gathering calls shows comparable results and exhibits several structural differences, thus, providing the potential for an interesting study on the aspect of context-dependent call variability.

7.3 Inter-specific acoustic variability in cryptic mouse lemurs and its biological significance

“Regarding design features, selection might favour (male) advertisement calls that provide relevant information about species identity…” and “… a perceptual system that is designed to discriminate conspecifics from heterospecifics.” (Hauser 1996, p. 369). Evolutionary theories (e.g. Templeton 1989; Andersson 1994) hypothesise that signalling as well as perception systems should have evolved for species recognition and discrimination relating to advertisement calls that might function as long distance cohesion calls between conspecifics for example in terms of mating, group cohesion or territorial defence. On the other hand, for other call types functioning in more general, not necessarily species-specific matters as for example alarm or aggressive calls, the necessity of species-specificity in signalling and recognition systems should be less important.

In the case of mouse lemurs acoustic studies did indeed revealed species-specific advertisement calls used in the context of mating (*mating calls*; Zimmermann and Lerch 1993; Hafen 1998; Zimmermann et al. 2000; Zietemann 2001); chapter 4 of this thesis) and during reunion of sleeping groups (*gathering calls*; chapter 4 of this thesis; own unpublished work on grey and Goodmans’ mouse lemurs). On the other hand, other call types did not show prominent structural differences: statistical analyses of short whistles that occur in attention and alarm contexts (Scheumann et al. in press) showed no species-specific call signatures (Zietemann 2001; Zimmermann et al. 2000).

Concerning call characteristics the species-specific advertisement calls of all three already studied mouse lemur species are broadband, frequency modulated trills of a comparable frequency band with nonetheless remarkable differences in the time-frequency contour. During mating as well as during group aggregation the accurate and fast recognition of conspecifics is highly important with regard to reproduction and predation especially in small, dispersed living cryptic species. Therefore, the structure of calls was optimized for detecting and localising the caller at the given time in virtually dense forest habitat (see chapter 4): they show a wide bandwidth, long call duration, high repetitive modulations of amplitude and frequency and were uttered in a moderate inter call interval as had been generally hypothesised for such calls (cf. Waser and Waser 1977; Wiley and Richards 1982; Norcross and Newman 1993).

Contrastingly, alarm calls predominantly do not have to allow or even should avoid a precise localisation of the sender. However, they need instead to be well adapted to their function in a given habitat with respect to morphological and behavioural constraints of the sender. Large primate species frequently use barks, often shrill ones to signal alarm. Quite the contrary, birds and prosimians (Andrew 1963; Scheumann et al. in press) are much more vulnerable to predators. Thus, these species predominantly use high-pitched thin whistles (Marler 1965) that are difficult to detect and localise for their predators. Also mouse lemur alarm calls are of the aforementioned structure (Zimmermann 1995b; Zimmermann et al. 2000; Zietemann 2001) and the used short whistles are predominantly above the hearing range or localisation abilities of their predators (cf. Zimmermann et al. 2000).

The conducted playback experiments (chapter 6) showed equal response strength of grey mouse lemurs towards conspecific, sympatric and allopatric alarm calls confirming a similar function of the three species’ short whistle calls, which had already been indicated in the statistical results. However, adequate responses towards alarm calls do not necessarily require identical vocalisations. Several studies in mammals showed that alarm calls of sympatric but not necessarily closely related species were known to be even functionally recognised by individuals (e.g. pipistrelle bats: Russ et al. 2004; diana monkeys: Zuberbühler 2000; vervet monkeys: Hauser 1988; Seyfarth and Cheney 1990; bonnet macaques: Ramakrishnan and Coss 2000; diurnal lemurs: Oda and Masataka 1996, Fichtel 2004). As in most of these cases the calls of the respective species differed markedly, an inter-species call recognition and importance can be assumed.

Experience is fundamental when recognizing heterospecific alarm calls, because only individuals who were familiar with the respective species responded towards the heterospecific calls (Ramakrishnan and Coss 2000). Thus, heterospecific signals that provide valuable information for a species might be learned and do not have necessarily to be coded for a specific sender or species but have to be functionally recognised and to cause a specific response.

In contrast to the short whistle calls the playback experiments revealed species-specific call recognition of the structurally different advertisement calls. In the first instance this may not be surprising but in other species the existence of hybrids shows that call differences are not in all cases sufficient to prevent interspecific matings (e.g. anurans: Blair 1958). Long-term studies of mouse lemurs in areas of sympatry have not revealed any hybrid forms until now (Radespiel pers. comm.). This fact, together with the results of the conducted playback experiments allows the assumption to be made that advertisement calls could represent an effective premating species-isolating mechanism (Ryan and Kime 2003) for the cryptic grey and golden brown mouse lemurs living in sympatry: Advertisement calls convey species-specificity and enable the mouse lemurs to minimise fitness loss in terms of searching time or hybridisation due to misunderstandings concerning potential mating partners.

7.3.1 The effect of sympatry and allopatry

Species-specific signalling and recognition are expected to be more relevant in areas where similar sibling or even cryptic species occur in sympatry than in those where a species has no further resembling species (e.g. Gerhardt and Huber 2002; Ryan and Kime 2003). It could be hypothesised that through reproductive character displacement acoustic signals representing such an isolating trait would carry more differences in sympatric than in allopatric species (Brown and Wilson 1956). According to Howard (1993) character displacement describes a pattern of greater divergence of an isolating trait in areas of sympatry between closely related taxa than in areas of allopatry.

In the case of advertisement calls functioning as mating signals during courtship in dispersed species, heterospecific calls of sympatric males have no biological relevance for the individuals. Quite the contrary, excessive response behaviour towards these calls could actually have a negative impact on the fitness of the individuals because they would risk energy loss due to unnecessary pursuits and contests/conflicts or even mismatings. On the other hand, conspecific mating calls may be vital for mate recognition. Due to these facts a clear difference between signal structure and recognition abilities in mating calls of sympatric species should be expected, especially in a non-hybridising area of the respective species. Calls of allopatric species do not necessarily have to show such prominent differences.

Indeed, the playback experiments conducted with grey mouse lemurs for this thesis (chapter 6) did not only show discrimination ability between conspecific and heterospecific advertisement calls; they even revealed a decrease in response strength from allopatric to sympatric calls. This result is consistent with the character displacement hypothesis although a final explanation concerning the evolutionary factors that forced these differences in response behaviour towards sympatric and allopatric calls can not be given yet (cf. chapter 6).

As was discussed in several previous publications the existence of reproductive character displacement, is hardly worth assessing (cf. Ryan and Kime 2003; Jang and Gerhardt 2006). In the case of mouse lemur advertisement calls significant evidence for such a mechanism would require further experiments to be carried out: the species-specific calls of mouse lemurs have to be additionally tested with grey mouse lemurs, which do not occur sympatrically with the golden brown species. If these individuals showed stronger responses towards the potential sympatric species of golden brown mouse lemurs than those already tested (which indeed occur in sympatry with them) character displacement could then be assumed to play a role in the evolution of perception processes on the advertisement calls in this genus.

Furthermore, even the evolution of call production resulting in the structure of advertisement calls should be examined in the light of this aspect. As discussed previously the different time-frequency contour of these calls might have evolved under a different natural selection pressure concerning habitat acoustic in relation to a different degree of relatedness between the three studied species (see discussion in chapter 4 for a more detailed analysis). Nevertheless, character displacement could have played a role as well in the evolution of call structural differences in these species.

In order to ascertain this hypothesis, calls from areas of sympatry should be compared with calls from areas of allopatry of two respective species. If character displacement were detected the structure of calls of both species would differ more strongly in sympatry than in allopatry. Unfortunately in the presented study we were not able to find a satisfying measurement for comparing the different advertisement calls. This was due to their completely different overall structure.

This problem did not arise in several previous studies on this aspect focussing on frogs (Höbel and Gerhardt 2003) or crickets (Honda-Sumi 2005; Jang and Gerhardt 2006). Namely, in these groups the loud calls show a much simpler overall structure: In contrast to qualitative differences in call structure of related species in several mammal species as for example bats (e.g. Pfalzer and Kusch 2003), dolphins (e.g. Steiner 1981) or non-human primates (e.g. Mitani 1987; Zimmermann 1990) these groups vary in other, rather quantitative call structure parameters. A ranging and comparison of these parameters such as a different chirp rate (Jang and Gerhardt 2006) is simple compared to qualitative differences in for example mouse lemur advertisement calls.

7.3.2 Evolutionary aspects of inter-species call variability in mouse lemurs

As mentioned in the introduction (chapter 3.4) mouse lemurs exhibit a high diversity of species. Species-specific acoustic signals may have played an important role in speciation processes of these small ancestral primates. Evolutionary theories hypothesise that a high selection pressure exists on sexual advertisement calls (e.g. Ryan and Kime 2003). Even for mouse lemurs it was revealed that these calls play an important role in reproduction (Craul et al. 2004).

Additionally, our playback experiments revealed very high response indices towards conspecific versus sympatric advertisement calls for females compared to males. Due to the low number of females (3 females as opposed to 13 males) this result can only serve as a guide and was therefore not presented in the results in chapter 6. However, this finding is consistent with the prediction that mouse lemur females especially should be interested in an conspecific mating partner due to their much higher paternal investment compared to the males (Martin 1972; Glatston 1979; Radespiel 2000; Eberle and Kappeler 2004a,b; Lutermann et al. 2006).

Thus, it is feasible that acoustic signals acted as prezygotic barriers to gene exchange in areas of overlapping and / or hybridisation (cf. Jones 1997) and that they had an important impact on the evolution of this genus. Genetic studies of sympatric mouse lemur species have revealed different types of sympatric reproductive isolation between two species. In the case of the grey and the Berthe's rufous mouse lemur (*M. berthae*) this seems to be the outcome of secondary contact of both species (Yoder et al. 2000). In another example the isolation of the grey and the grey-brown mouse lemur (*M. griseorufus*) might have evolved sympatrically on the basis of ecological distinctions and mate recognition signals (Yoder et al. 2002).

Sympatric speciation has been discussed very controversially, but considered more and more in the last decades (cf. Via 2001) since theoretical studies using computer models showed adequate results as well (e.g. Turner and Burrows 1995, Johannesson 2001). An investigation into the possible speciation processes of the three study species is an interesting topic for understanding general primate evolution processes and is already a current subject in phylogenetic analyses (Radespiel pers. comm.).

7.4 Inter-specific comparison of the acoustic variability between mouse and sportive lemurs

The presented studies have shown not only similarities, but differences as well between loud calling behaviour in the two study species. First of all, sportive as well as mouse lemurs uttered several different vocalisations during dispersal and reunion. Thus, as expected, in both nocturnal lemur species loud calling represents an important aspect for communication.

All recorded call types showed a frequency modulated structure the whistles of mouse lemurs being an exception. The latter were assumed to have an alarm and attention function (Scheumann et al. in press) which might explain this call structure. For the other call types the mentioned modulations are extremely broadband, covering frequency ranges up to 6 kHz for sportive lemurs (chapter 5) and 20 kHz for mouse lemurs (chapter 4; Zimmermann 1995a; Zietemann 2001). Most call types contain several modulations or are uttered in series. All these call characteristics provide good detection and localisation abilities for conspecifics (see chapter 4) as “the purpose of long distance signals” (…) “is to advertise the presence of the sender to a receiver” (Ryan and Kime 2003).

However, the frequency ranges of recorded vocalisations differed markedly between the two species: sportive lemur calls were between 0.5 kHz at a minimum and 6.0 kHz at a maximum (chapter 5) while the vocalisation of mouse lemurs ranged between 8.0 – 40.0 kHz (Zimmermann and Lerch 1993; Zimmermann 1995a; Zietemann 2001; Zimmermann and Hafen 2001; chapter 4+6). On the one hand these differences can be explained by the fact that sportive lemurs are much larger than mouse lemurs: their weight is approximately the 15-fold than that of the mouse lemurs (see chapter 3.4).

The production of sounds depends on **morphological constraints**; therefore these frequency differences are not surprising (see chapter 7.1.2). Furthermore, a different ***predation pressure*** might explain these species differences. Although both studied species shared the same habitat and their predators do not differ markedly (Goodman 2003), the predation pressure on mouse lemurs was assumed to be much higher than that for the larger nocturnal species. Mouse lemurs are highly vulnerable during the night and day, whereas, sportive lemurs are predominantly at risk during the day (Goodman 2003). Therefore, the need for inconspicuousness even in calling behaviour might reflect a basic driven force of natural selection in the small mouse lemurs towards high frequency sounds. These can not be heard by birds, owls included, which are one of their predominant predators besides snakes which can not hear at all (Fay 1988; Hauser 1996; Goodman 2003).

In both species males as well as females were involved in uttering calls (chapter 4+5). Due to the fact that long distance calling represents a costly behaviour (e.g. Bradbury & Vehrencamp 1998; Wich and Nunn 2002), both sexes should have advantages from calling. This seems to be reliable for both species, although calling behaviour was hypothesised to have different functions in the light of their different social systems. (A detailed discussion on this aspect will be given in chapter 7.4.1). However, the cohesion of sleeping and mating partners is of paramount importance in both species and should be independent of sex.

A further difference between the species is the fact that in Milne Edwards’ sportive lemurs, males and females shared only one call type whereas the other call types were sex-specific. Contrastingly, in golden brown mouse lemurs all call types were used by both sexes, this also being the case for grey mouse lemurs (Zimmermann 1995a; Zietemann 2001; own observations).

This could assume a different function of sex-specific loud calling and will be discussed in the context of their different social systems in the next chapter (7.4.1).

7.4.1 Biological function of loud calls – the effect of social organisation

In a variety of taxa such as insects (e.g. Ryan and Wilczynski 1988), frogs (e.g. Gerhardt 1994; Ryan 2001), and birds (e.g. Catchpole and Slater 1995) as well as in primates (e.g. Waser 1982; Hohmann and Fruth 1995; Zimmermann 1995b; Geissmann 2002) long distance calling represents a fundamental tool for social communication. According to the socio-ecological model (Crook 1970; Emlen and Oring 1977; Terborgh and Janson 1986) there exist different selection pressures affecting the distribution of males and females determining their individual success of survival and reproduction. This success is usually limited for females by the access to critical resources and predation pressure whereas that of males is mainly limited by the access to fertile females (Trivers 1972; Clutton-Brock and Harvey 1977; Emlen & Oring 1977).

The social organisation of a species is therefore influenced by the outcome of several different properties of individual behavioural interactions and strategies (Hinde 1976). Acoustic variability should be greatly affected by the social requirements of a species - it should be determined by the individual interactions and strategies of the individuals. The acoustic variability should differ between species living in different social systems, even when they inhabit the same ecological community such as our investigated species.

The social organisation of the *Milne Edwards' sportive lemurs* was described as dispersed monogamy (Müller and Thalmann 2000). The home range of one male coincides with the range of one female and partners show territorial behaviour (Rasoloharijaona et al. 2003; this thesis chapter 5). Thus, sex-specificity and individual signal structure of calls (chapter 5) could allow individual recognition of the (mating) partner on the one hand and sex-specific recognition of potential competitors on the other hand.

This coincides with the assumption that the loud calling behaviour of the Milne Edwards' sportive lemurs functioned as a ritualised aggressive display of pairs for territory defence (see chapter 5). The duetting loud calling behaviour at the beginning and the end of their activity period involved both males and females due to their social relatedness and dependency. Additional observations revealed that this acoustic behaviour also occurs in the further course of the night albeit less frequently (Rasoloharijaona pers. comm.; own observations). In sportive lemurs both partners are interested in resource competition and a stable pair-bonding: males can be relatively sure of a mating partner and females can profit from help in resource and offspring defence. Thus, antiphonal calling of partners allows territory and partnership display towards neighbouring pairs and enables cohesion of the dispersed partners within a pair.

Golden brown mouse lemurs live in a multi-male/multi-female system with a promiscuous mating pattern (Weidt et al. 2004). Species-specific advertisement calls were also uttered during dispersals and reunions but we assumed that these calls adopt different functions during these two situations: During dispersal of groups, male strangers were present and uttered advertisement calls while passing by the sleeping site or chasing another individual of the observed group. In golden brown (own observations) and in grey mouse lemurs (Schmelting 2000; own observations) it was observed that calling males inspect sleeping sites for oestrous females, and in many cases males showed this behaviour during several consecutive evenings.

During some additional morning observations at the sleeping sites of golden brown as well as of grey mouse lemurs and during focal observations in the course of the night also mating advertisement calls of male strangers following a female were noted. This would imply that this behaviour particular male behaviour does not simply represent a dispersal activity. We concluded that these calls are mating calls (chapter 6), coinciding with the assumed promiscuous mating pattern in the multi-male/multi-female organisation.

In this context call signatures encoding for fitness parameters might provide valuable information for a potential mating partner (cf. Zimmermann 1995a). This might be an interesting topic for further acoustic analyses. Contrastingly, during reunion of sleeping groups advertisement calls were assumed to function as gathering calls. In this context these calls were uttered by males and females and even occurred in groups consisting solely of females.

In the view of group re-aggregation the obtained group-specific signatures of gathering calls (chapter 4) could allow the detection, discrimination and localisation of group members. Furthermore, it seems possible that also individual signatures exist among golden brown mouse lemurs (Polenz 2000) as shown for grey mouse lemurs (Zimmermann and Lerch 1993). This may provide individual recognition within a system of individualised neighbourhood (Radespiel 2000; Weidt et al. 2004).

In contrast to the Milne Edwards' sportive lemur a resource defence function of mouse lemur loud calls could not be found. However, Radespiel (2000) and Weidt et al. (2004) assumed that the home range overlap in mouse lemur sleeping group partners was larger in co-sleeping than in other individual dyads indicating some amount of spatial separation of sleeping groups.

The presented study of this thesis (chapter 4) has also indicated an exclusive usage pattern of sleeping sites for the observed golden-brown mouse lemur groups (see also Weidt et al. 2004). In contrast to the Milne Edwards' sportive lemur this kind of spatial separation of sleeping groups was assumed to have been achieved through intensive marking activities at the sleeping sites during the dispersal of groups. Hence, mouse lemurs also show some kind of territory defence for these resources, which are essential for survival (Radespiel et al. 1998).

Due to the fact that in the Milne Edwards' sportive lemur marking behaviour, that might also fulfil territorial functions is totally lacking (see chapter 3.4), calling behaviour might have occurred during dispersal and reunions of pairs (and even in the time between). Apart from this symmetric distribution of loud-calling the structure of calls also gives an indication of the loud call function as territory display signals: the noisy parts of sportive lemur calls imply a rather aggressive context for the respective calls (Morton 1977, 1982; Ehret 2006). A detailed context analysis of Milne Edwards' sportive lemur call types and tests concerning their function by way of playback experiments is part of a current PhD-thesis (M. G. Mendez Cardenaz) and will provide further information on this topic.

7.5 Evolution of long distance calls in primates

As discussed in the previous chapter the social organisation of a species influences its acoustic variability – including signal function – due to the fact that different social organisations require different communication aspects. Therefore, it can be assumed that the evolution of "higher", complex social systems involves the evolution of social calls and their respective functions.

(Müller and Thalmann 2000) hypothesised that a dispersed multi-male/multi-female system derived from promiscuity, representing the ancestral pattern for mammalian social organisation should be regarded as the ancestral condition for primates. Furthermore, it was assumed that the shift from nocturnal to diurnal activity has involved the change from solitary foraging to foraging in cohesive groups (Martin 1981; van Schaik 1983; van Schaik and van Hooff 1983).

Solitary nocturnal as well as diurnal gregarious primate species use calls, which function as cohesion calls over long distances: in solitary ranging species individuals utter long distance calls in order to find an adequate mating partner (e.g. Sterling 1993; Zimmermann 1995a). In contrast, loud calls of gregarious primates do not necessarily have to fulfil this courtship function. They are, instead, substantial tools implemented by the group members so as to remain in contact (see chapter 3.2). It can be hypothesised that group cohesion calls of higher primate species with complex social systems may originate from mating calls of ancestral primate species living in more basic social organisations.

Due to the fact that lemur species have undergone unique adaptive radiation resulting in various degrees in social organisation including nocturnal as well as diurnal species, they represent ideal models to gain insights into the evolution of long calls: Females of the aye-ayes (*Daubentonia* *madagacariensis*), a solitary ranging lemur species that does not form any sleeping associations utter oestrus advertisement calls to attract males during their short receptive period (Sterling 1993; Sterling and Richard 1995).

Thus, even in this primary state of social organisation mating calls play an important function in this nocturnal species. In addition, the solitary ranging species of the genus *Microcebus* constitutes a contemporary living ancestral state in the primate evolution. However, in contrast to the aye-ayes they have evolved long-term sleeping group associations. This thesis shows that mouse lemurs do not only use advertisement calls as mating calls but also as gathering calls for sleeping group coordination (chapter 4). In these species long calls of the same structure were used for two different functions concerning cohesion aspects of conspecifics. This could assume an advancement of the mating calls in order to fulfil "new" functions in a more complex social society.

Individuals of species which live as a dispersed pair (or group) in stable, exclusive territories as the Milne Edwards' sportive lemurs do, do not necessarily need to make any loud calls for courtship behaviour. These individuals do not have to remain in loose contact while foraging and have to defend their territory against conspecifics. As already demonstrated in this thesis (chapter 5), Milne Edwards' sportive lemurs frequently used long calls for pair cohesion (inter-group) and spacing (inter-group) situations.

The nocturnal wolly lemurs that live in permanent pairs, foraging and sleeping together, use vocalisations as well that were assumed to function in group cohesion and others that may be involved in inter-group spacing (Petter and Charles-Dominique 1979; Harcourt 1991). Furthermore, this species made quiet purring calls during group travelling and foraging. A detailed analysis of call function in sportive as well as in woolly lemurs has not been made to date. But, it might be possible that group cohesion and territorial calls represent a different branch of long call evolution.

An interesting aspect on this topic is represented by the fact that in contrast to aye-ayes and mouse lemurs, sportive and wolly lemurs do not exhibit distinct marking behaviour. In the case of the golden brown mouse lemur marking was assumed to act as some kind of resource defence – by intense sleeping site marking at the beginning of their activity period (see chapter 4). It could be possible that in nocturnal arboreal lemur species, which defend real territories, this olfactory behaviour, has been replaced by vocal behaviour.

Figure 7-2 illustrates long call evolution in primates hypothetically. However, for a more meaningful hypothesis further, more detailed analyses are necessary, taking a lot more species other than lemurs into account.

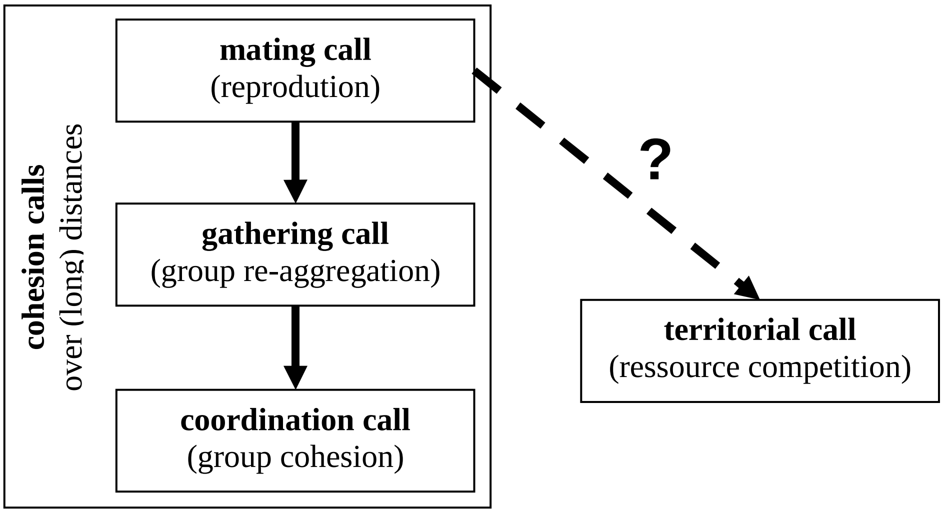

Fig. 7-2: Hypothetical passing of primate long distance call evolution. The cohesion calls might not only function in long distance communication but partially also in short distance communication.

7.6 Concluding remarks

As has already been demonstrated for aspects of social and mating systems (cf. Schülke and Ostner 2005) even communication facilities of nocturnal lemurs are a lot more complex than has been previously thought. Individualised relationships such as the sleeping groups in mouse lemurs and the dispersed pair bonding of sportive lemurs require well-defined communication skills in these ancestral primates.

Different call variability and biological functions of vocalisations in the two studied species have evolved in accordance with different requirements of their social systems, used resources and predation pressures. Inter-specific call differences of specific acoustic signals, which are essential for individual reproduction, may have a strong influence on species continuity or diversification from an evolutionary point of view.

The results of two species of ancestral primates have revealed the following: Communication signals may, on the one hand have an important impact on speciation processes and may enable the evolution of “higher” societies with complex social networks on the other hand. Thus, the study of non-human primate communication gives intellectual light to fundamental aspects in the evolution of primate societies – including our own, the human society.

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10 Professional development

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