SOCIALITY AND COMMUNICATION IN WOOLLY LEMURS

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This work was carried out only through the mercy of God.
To God be the Glory, both now and forever!!
FOREVER AND EVER

To
my parents
my brother
my sister
my niece
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Malagasy western woolly lemurs (*Avahi occidentalis*) are pair-living, weasel-sized nocturnal lemurs, with a specialized plant diet that makes it nearly impossible to keep and breed them in captivity. Endangered by the destruction of their natural forest habitat, they are classified as endangered by the IUCN. Whereas feeding ecology and locomotor behaviour of the western woolly lemur have already been described, only scarce information on their socioecology is currently available. The aim of my thesis is to provide the first empirical data on sleeping site ecology, social relations, female dominance, and acoustic communication of woolly lemurs, thus embedding them into the evolution of sociality and communication in primates and providing a foundation for establishing management strategies.

The choice of a sleeping site is crucial for individual survival. Season may have strong effect on vegetation and thus on the availability of suitable sleeping sites and predation risk in arboreal primates. Therefore, in chapter 2, I explored how seasonality influences the characteristics and usage of sleeping sites by GPS-based radiotelemetry of six lemur pairs. Each woolly lemur used a total of 19 to 41 different sleeping trees over the whole study period and preferred to sleep either on branches or in the tree crown with dense foliage. Height and usage of a sleeping site varied according to the season. During the late dry season, woolly lemurs preferred sleeping sites that were 5-10 m high while there was no height class preference during both early dry and early rainy season. Moreover, the focal individuals switched between sleeping trees more frequently during the early dry and early rainy season than during the late dry season. Woolly lemurs showed a stable sleeping group composition during the study: a group was composed of a focal pair and its offspring. Our results confirm that sleeping site ecology of woolly lemurs is strongly affected by season. Sleeping site choice depends on vegetation cover most probably shaped by the need for thermoregulation and predator avoidance. Pair-specific usage of sleeping sites is independent of season and implies inter-pair competition for suitable sites and sleeping site territoriality throughout the whole study period.

Peaceful relations among pair partners are fundamental components of a harmonic social life in all human societies. In nonhuman primates, research on the evolution of the
peaceful side of social life is largely neglected. In chapter 3, I studied social interactions in a pair-living lemur of Madagascar, the western wooly lemur (*Avahi occidentalis*) to better understand pair relations of socially monogamous nonhuman primates. By means of radio-tracking, we observed interactions of six pairs of this species during the night in the dense tropical forest of northwestern Madagascar for a period of eight months. Based on more than 870 hours of focal observations, we discovered that interactions between pair partner were extremely peaceful. The rate of affiliation was significantly higher than the rate of agonism. The revealed rate of 0.01 agonistic events /h is the lowest rate of agonism between pair partners in all studied primate species so far. Nevertheless, when a rare event such as an agonistic conflict happened, it was exclusively initiated and won by the female. Thus, female dominance prevails, even in an extremely peaceful lemur.

A central question in primate socioecology is how individuals govern distribution in time and space. One important mechanism for nocturnal primates living in dense tropical forest is acoustic and olfactory communication. In Chapter 4, I investigated to what extent a nocturnal pair-living primate species relies on vocalizations for social communication. We followed six pairs of western woolly lemurs from May to December 2008 by GPS-based focal animal sampling with continuous recording. We determined the focal animal’s geographic position using a Global Positioning System. We recorded vocalizations from focal individuals using a microphone connected to a tape recorder. Using common bioacoustic techniques we revealed three acoustically distinct and frequently used call types: the ava-hee call, the whistle call and the growling call. The ava-hee call is a loud call produced mostly in the vicinity or at the boundaries of a territory, suggesting a function in territory demarcation. The whistle call is a loud, harmonic call, given between pair partners during locomotion. It leads to a reunion of pair partners supporting a function in pair cohesion. The growling call is a soft and noisy call consisting of rapidly repeated short broadband pulses, produced in response to an approaching pair partner or other species such as sportive lemurs or brown lemurs. It most likely acts as threatening call. Thus, under conditions when visibility between bonded pair partners is poor, such as in tropical forests, low visibility may select for acoustic communication providing an important mechanism governing distribution of individuals in time and space.

All in all, this thesis provided first empirical data on sleeping site ecology, social behaviour and communication of a previously barely known lemur species. It shows that this nocturnal pair-living lemur displays distinct differences, but also specific universals relative to its diurnal relatives. Furthermore, findings suggested that woolly lemurs are highly
threatened by human poachers, in particular during the dry season, a fact to be considered in future conservation programmes.
ZUSAMMENFASSUNG

Titel: Sozialität und Kommunikation bei Wollmaki
Name: Rindrahatsarana Ramanankihina


Untersuchungszeitraums nahezu exklusiv von gleichen Paar benutzt. Dies weist auf Konkurrenz zwischen den Paaren für geeignete Schlafplätze und auf Territorialität hin.


Laut wird abgeben, wenn sich Paarpartner annähern, aber auch andere Arten, wie zum Beispiel Wieselmakis oder Braune Makis, zu nahe kommen. Es scheint sich beim "growling" Laut um einen Drohlaut zu handeln. Für paarlebende nachtaktive Arten, die in Habitaten wie dichten tropischen Wäldern leben, scheint die akustische Kommunikation im besonderen Maße selektiert und ein wichtiger Mechanismus zu sein, der die Verteilung der Individuen in Raum und Zeit beeinflusst.

CHAPTER 1

GENERAL INTRODUCTION
1. Biodiversity in Madagascar

The megadiverse countries are a group of countries which hold many unique species and are therefore considered to be the richest in the world in terms of biodiversity. The World Conservation Monitoring Centre recognized 17 megadiverse countries in July 2000 (Figure 1). These countries include areas of high biodiversity importance as well as degraded land and urban areas (MITTERMEIER et al. 1997). The idea of megadiversity countries was initiated by the primatologist Mittermeier in 1988, from a preliminary analysis of priorities regarding the protection of primates in the world. He found that four countries had, alone, two-thirds of primate species. The first four mega-diversity countries are Brazil, Indonesia, Madagascar and Congo. These countries had the highest levels of endemism: 100% of lemurs in Madagascar are endemic, and levels of endemism in Brazil and Indonesia are also surprisingly high (MITTERMEIER 1988). It should also be noted that there is a significant overlap between megadiverse countries and biodiversity hotspots in the world: the whole territory of many nations, or any part of them, is recognized as centers of both biodiversity and threats (JACQUET u. TUBIANA 2008).

Figure 1: Map showing the 17 megadiverse countries (green) as identified by the World Conservation Monitoring Centre (source: wikipedia: http://en.wikipedia.org/wiki/Megadiverse_countries).

Madagascar is identified as a megadiverse country and biodiversity hotspot (MYERS et al. 2000). This is linked to the high degree of diversity and endemism and also to the
ongoing threats of natural communities. Madagascar, an island of only 587,000 km², is considered as one of world's highest priorities in biodiversity conservation. Levels of endemism among plants, vertebrates, and invertebrates are stunning. The most renowned group is the lemurs.

Lemurs are emblematic of Madagascar’s biodiversity. These prosimians primates are classified in seven families, two of them recently extinct. The living families are: Indriidae, Lepilemuridae, Cheirogaleidae, Daubentoneidae, and Lemuridae. By their activity pattern, lemurs are classified as diurnal (active during the day), nocturnal (active during the night), or cathemeral (active night and day). Loss of habitat and fragmentation of the forest are among the biggest threats to lemurs (MITTERMEIER et al. 2006). It was estimated in 2010 that 90% of the forest cover in Madagascar has disappeared in favor of slash-and-burn agricultural activities, animal husbandry, mining industries, charcoal production, and cut of rare woods (MITTERMEIER et al. 2010). The lemurs over the centuries of evolution which had conquered all the ecological niches of Madagascar, occupy only 10% of the Malagasy territory, 60,000 km² (PETTER et al. 1977). Moreover, if we look at the distribution of individual species, there are additional restrictions due to specific ecological requirements for particular species. A new assessment of these primates reveals that Madagascar has the highest proportion of threatened species of any primate habitat region or any country in the world (IUCN Red-List Workshop 2012). Twenty three of the species are now considered as critically endangered, 52 endangered and 19 vulnerable on the IUCN’s Red List of Threatened Species.

2. The largest Malagasy lemurs – the taxonomic family Indriidae

Among the five living families of lemurs, the family Indriidae contains the largest bodied members of all lemurs (GLANDER u. POWZYK 1995). The family is also the most diverse in terms of social system and activity pattern. The social systems are either described as cohesive pairs (HARCOURT 1991; WARREN u. CROMPTON 1997; JOLLY 1998; THALMANN 2001) or as multi-male multi-female group (RICHARD 1978; JOLLY 1998). The activity pattern is either diurnal or nocturnal. The two diurnal representatives are Propithecus sp, and Indri sp and the only nocturnal member is Avahi sp. All Indriidae are characterized by elongated hind legs that allow them to move by leaps between vertical support, made by a sudden expansion of their long hind limbs and powerful thighs, referred as
“vertical clingers and leapers” (PETTER et al. 1977). The tail of Propithecus and Avahi are relatively long while that of Indri is merely a stump. Indri and Propithecus are the largest living lemur species (GLANDER u. POWZYK 1995). Their social behavior is well studied (RICHARD u. HEIMBUCH 1975; POLLOCK 1979; KUBDZELA et al. 1992; MEYERS 1993; BROCKMAN et al. 1998; POCHRON et al. 2003). Females show an agonistic superiority over males across different contexts, referred to as unambiguous female dominance. Their vocal communication is also well described (PETTER 1962; POLLOCK 1975; PETTER u. CHARLES-DOMINIQUE 1979; POLLOCK 1986; THALMANN et al. 1993; MACEDONIA u. STRANGER 1994; MARETTI et al. 2010; FICHTEL u. KAPPELER 2011). The song of Indri is extensively studied in the field. The main functions are related to territorial announcement and defense (PETTER et al. 1977; PETTER u. CHARLES-DOMINIQUE 1979; POLLOCK 1986; GEISSMANN u. MUTSCHLER 2006). Other than the song, the vocal repertoire of Indri contains 8 vocal types uttered by the adults (POLLOCK 1975; PETTER u. CHARLES-DOMINIQUE 1979; MARETTI et al. 2010). Calls are given in series or associated with other vocalizations. Indris vocalize in the context of predation, foraging, resting, traveling, agonistic, and vigilance contexts. In Propithecus, for example, the alarm calls are extensively studied (e.g. FICHTEL u. KAPPELER 2011). Before and during group progression, Propithecus produce grumble vocalizations (TRILLMICH et al. 2004).

Whereas the two diurnals Indriidae have been well studied with respect to sociality and communication, there is a lack of information for the only nocturnal representative of Indriidae, the Avahi. Avahi are difficult to investigate under natural conditions owing their cryptic lifestyle (GANZHORN et al. 1985), which makes observations and data collection extremely difficult. In order to embed the group of Avahis into the evolution of sociality and communication of primates and to establish conservation strategies, knowledge on their biology is urgently needed.

3. Woolly lemurs as models

Woolly lemurs are the smallest of the family Indriidae. They are considered to be the most ancestral of the living Indriidae (ALBIGNAC 1981; RUMPLER et al. 1983, 1988). They have a dense coat, curly or woolly appearance of the dense fur, hence the name woolly lemur (THALMANN 2003). Woolly lemurs are readily identified by the white patches on the backs of their thighs, which is the origin of the Malagasy name “fotsife”. These lemurs have
been considered to be monogamous, living in small family groups usually composed of an adult male and female, and their immature offspring (ALBIGNAC 1981; GANZHORN et al. 1985; HARCOURT 1991). They frequently rest closely huddled together, a behavior rarely observed in the other similar sized nocturnal species. They are unique in combining nocturnality, pair-living, and folivory (GANZHORN et al. 1985). Initially a single species, *Avahi laniger*, with an eastern and western subspecies was recognized (PETTER et al. 1977). Afterwards, both subspecies were advanced to full species, *Avahi laniger* and *Avahi occidentalis* based on cytogenetic characters (RUMPLER et al. 1990). Recent molecular investigations have increased the number of species to nine (ANDRIANTOMPOHAVA et al. 2007). We chose one species of woolly lemurs for our project. Our study model was western woolly lemurs (*Avahi occidentalis*) (Figure 2).

![Image of woolly lemurs](image.jpg)

**Figure 2**: The woolly lemur (*Avahi occidentalis*) in the Ankarafantsika National Park (photo taken by Marine Joly).
The weight of this species ranges from 700 to 900g (THALMANN u. GEISSMANN 2000; THALMANN 2001). The fur colour of body is brown or grey. The face is pale forming a characteristic mask. The contrasting facial mask and dark eye-rings distinguish them from other species of woolly lemurs (THALMANN u. GEISSMANN 2000). Their tail has a length about 31-37cm, which is longer than the combined head-body length (MITTERMEIER et al. 2010). The breeding season occurs from March to May. Infants are born during September and October. The baby stays with its mother and is carried on the front of the mother for 2 months. Then, the baby moves from the front to the back and begins slowly to venture away from the mother (personal observation). Western woolly lemurs are distributed in a restricted area to the north and east of the Betsiboka River as far as the Bay of Narinda (THALMANN u. GEISSMANN 2000, Figure 3). They occur in the Ankarafantsika National Park, Bora Special Reserve, and the Mariarano Classified Forest (NICOLL u. LANGRAND 1989, RANDRIANAMBININA et al. 2003).
By the IUCN red list 2012, western woolly lemurs are classified as endangered. Habitat loss is the major threat for these lemurs (MITTERMEIER et al. 2010). They function
as a prey species for various predators (Aerial predators: *Accipiter henstii, Eutriorchis astur, Polyboroides radiatus*: Terrestrial predators: *Cryptoprocta ferox*) including humans (GARCIA u. GOODMAN 2003; SCHEUMANN et al. 2007). Their primary wild predators are Henst’s goshawks and fossa, which find them while resting on exposed branches during the day (Figure 4).

![image](image.png)

**Figure 4**: Major predators of woolly lemurs are Henst’s goshawks (*Accipiter henstii* (a)) and fossa (*Cryptoprocta ferox* (b)), photos taken from Arkive ([http://www.arkive.org/hensts-goshawk/accipiter-henstii/](http://www.arkive.org/hensts-goshawk/accipiter-henstii/), [http://www.arkive.org/fossa/cryptoprocta-ferox/image-G64982.html](http://www.arkive.org/fossa/cryptoprocta-ferox/image-G64982.html)).

Western woolly lemurs rest together in trees with dense foliage. WARREN u. CROMPTON (1997) noticed that the lemurs changed their sleeping sites when exposed to the sun later in the day. No further information is available concerning the characteristics and usage patterns of woolly lemur sleeping sites. Because sleeping sites are an important resource for the survival of this species, we focus our research (presented in chapter 2) on sleeping site ecology. This knowledge is urgently needed for the conservation of this species.

Social behavior in western woolly lemurs is poorly understood. Adult males and adult females are socially and spatially associated and have frequent interactions, which categorized them as a cohesive pair-living lemur. Affiliative and agonistic interactions between male and female have not been quantitatively or extensively studied. WARREN u. CROMPTON (1997) saw four occasions of allogrooming during their 560 hours of observation. Thus, in the chapter 3, we will give first quantified information about the affiliative and aggressive interactions in this species.
Until now, little has been known about the vocal communication of Avahi. In total, three types of calls have been noticed to be produced by woolly lemurs: ava-hee, whistle and growling calls (Petter u. Charles-Dominiques 1979; Harcourt 1991; Warren u. Crompton 1997). The information available is only a description of the calls emitted by woolly lemurs. The function proposed by these authors of the three types of call is still controversial. No contextual or acoustic analysis has been conducted. Therefore, in chapter 4, we studied vocal communication in this endangered species to assess the role of acoustic communication for inter-pair spacing and intra-pair cohesion and coordination.

4. General aims and hypotheses of my thesis

As outlined before, western woolly lemurs are highly threatened by the destruction of their natural forest habitats and their small distribution. Conservation of this species by captive breeding is complicated by the fact that woolly lemurs are specialized folivores and can not be maintained and bred in captivity (Petter et al. 1977; Harcourt u. Thornback 1990). Consequently, more information on the biology and life history of this poorly known nocturnal lemur is highly needed.

Thus, I aimed to enhance our current knowledge on sociality and communication of woolly lemurs by focussing on the three major topics which follow:

a. Sleeping sites and their significance for survival in primates

Sleeping sites are an important resource for animals. Resources can be defined as all supplies of the environment that are consumed or used for the purpose of increasing the survival, growth, and maturation of individuals and their offspring (Begon et al. 1990). Primates spend over half of their life in their sleeping sites (Heymann 1995; Meddis 1983). Therefore, the choice of a sleeping site may be crucial for individual survival (Cowlishaw 1994). In primates, variability exists in sleeping sites where the animals spend their inactive periods. Among the nocturnal prosimians, species use nests, tree holes or hollows, and open vegetation for sleeping during the day (e.g. Radespiel et al. 1998; Bearder et al. 2003; Radespiel et al. 2003; RasoloHarijaona et al. 2003;
Western woolly lemurs are known to sleep in open vegetation. They are discrete and hide themselves in dense vegetation during daytime. They occupy the dry seasonal forest. In the dry season, 50% of the trees shed their leaves (RAMANGASON 1988) once per year at the approach of the dry season. Some species stay green for about four months, while others lose the last of their old leaves only when the new ones unfold, which happens in all species shortly after the rain begin (JEKINS 1987). Season might be among the major factors which influence the choice of sleeping site in western woolly lemurs. Sleeping trees of animals may determine their vulnerability to predators and/or to anthropogenic disturbances.

Available studies of sleeping site usage by woolly lemurs are lacking. This situation is unfortunate because information on this topic may be directly relevant to conservation planning. To fill this gap of knowledge, in chapter 2, we investigated sleeping tree choice by western woolly lemurs at Ankarafantsika National Park. We explored how season influenced sleeping site characteristics and usage pattern in a nocturnal lemur sleeping in open vegetation in dry deciduous forest, and what this implies for conservation. We collected daily data on the quality, number of sleeping sites, patterns of use and reuse, and sleeping group composition in the dry and rainy season. We described sleeping group composition and usage of sleeping sites. Our prediction was that western woolly lemurs might be vulnerable to predators and/or humans during the dry season when the trees shed their leaves.

b. Social interactions, dominance, and their role in primate social systems

Social interactions between sexes represent an interesting situation to consider the balance between cooperation and conflicts for species living in groups (CROOK 1970, WALTERS u. SEYFARTH 1986). Male and female interactions include both the sexual and nonsexual contexts. In the latter, male and female social relationships are characterized by a combination of affiliative and aggressive interaction. Affiliative interactions represent the overwhelming majority of primate social interactions, and form the basis of individual social bonds. With regard to diurnal primates, group living prosimians, new and old world monkeys and apes spent most of their social time in affiliation, driving by mutual benefits received from the collective environments of living in stable groups (SUSSMAN et al. 2005). Agonism
occurs at very low frequencies. It occurs for less than one percent of the activity budget of diurnal lemurs (SUSSMAN et al. 2005).

Based on the outcome of agonistic encounters and affiliative interactions, dominance relationships between and within sexes can be assessed (FORNASIERI u. ROEDER 1993; ROEDER u. FORNASIERI 1995; RADESPIEL u. ZIMMERMANN 2001; OVERDOFF et al. 2005). Dominant animals have been found to receive the greatest amount of affiliative behavior from other individuals (KERBY u. MACDONALD 1988). Unlike any other group of mammals, most lemurs exhibit some form or degree of female dominance, where males generally behave submissively to adult females (JOLLY 1984). Thus, lemurs provide a unique context for examining the evolution of female dominance.

While intra-pair relations in diurnal representatives of the family Indriidae are well studied and suggested unambiguous female dominance (RICHARD u. HEIMBUCH 1975; POLLOCK 1979; KUBDZELA et al. 1992; MEYERS 1993; POCHRON et al. 2003), information on nocturnal Indriids is lacking so far. Therefore, in chapter 3, we examined social interactions between pair partners in woolly lemurs, taking the western woolly lemur (Avahi occidentalis) as a model. We examined the extent to which phylogeny, activity mode, or the cohesiveness of pair partners shaped the quality of social interaction. We determined the rate of affiliative and agonistic behaviors between pair partners. If female dominance represents an ancestral trait in the family of Indriidae, we expect that western woolly lemurs will show the same pattern of social relations between sexes as their diurnal relatives living in either pair or multi-male multi-female systems.

c. Acoustic communication and its role in primate social systems

Primates live often in dense tropical forests, where the visibility is extremely low. Vocalizations are thus one of the primary mechanisms by which animals may govern dispersion and cohesion in space and time. Acoustic communication is an efficient mechanism for the transmission of social and environmental information, as dense vegetation limits the transmission of visual signals. Thus, knowledge of vocalizations helps us to know the interaction of the animal and the surrounding area (CHENEY u. SEYFARTH 1990; BRADBURY u. VEHRENCAMP 1998). Data characterizing vocal repertoires and the contexts of calling has been collected from many primate species. These data have contributed to assessing the role of acoustic communication in primate social systems. A large
part of the communication between social individuals is used to control their spatial relationships (TINBERGEN 1959; MARLER 1968). Among primates, variable vocal signals are characteristic of short range communication within groups, whereas stereotyped vocalizations occur more often in long range interactions between groups (MARLER 1965; GREEN 1975). Taking into account their spacing functions, primate loud calls present an acoustic adaptation to increase their propagation over distance (WASER u. WASER 1977). Nonhuman primates produce loud calls at relatively low frequencies and with high production rates or they contain a repeated part or harmonic structure to facilitate their transmission over long distances (WASER u. WASER 1977; RICHARDS u. WILEY 1980; ZIMMERMANN 1995; MITANI u. STUHT 1998).

Primate vocalizations carry different information. They encode information about the identity, sex, and age of the calling animals (e.g. CHENEY u. SEYFARTH 1990; RENDALL et al. 1996), reproductive status (e.g. FITCH 1997), events in the environments (BUGNYAR et al. 2001; MAYNARD SMITH u. HARPER 2003; FITCH 2008). For example, the alarm calls of monkeys and ring-tailed lemurs provide semantic information about the signaler’s current physical states, the type of predator, and the degree of threat (SEYFARTH ET AL. 1980; SAUTHER 1989; CHENEY u. SEYFARTH 1996; TEMPLETON et al. 2005). Chimpanzee screams conveyed information about the nature of the conflict (SLOCOMBE u. ZUBERBÜHLER 2007). Vocalizations are used in many different contexts, with members of their social group or non-members, such as territorial defense, pair bonding, mate guarding, group coordination, alarm call, and many other facets of an organism’s social life. Many of them are loud enough to be heard at a distance (WINTER et al. 1966; GREEN 1975). Until now, knowledge on woolly lemur communication is poor and limited to onomatopoeic descriptions of calls. Thus, in the chapter fourth, we acoustically characterize most frequent vocalizations of woolly lemurs by means of bioacoustics and relate for the first time acoustic structure of vocalizations to their postulated function. Findings of this study provided more information about how the acoustic communication governs inter- and intra-pair spacing in primates.
CHAPTER 2

SEASONAL EFFECTS ON SLEEPING SITE ECOLOGY IN A NOCTURNAL PAIR-LIVING LEMUR (*Avahi occidentalis*)


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**Contribution to the work**

I participated in the design of the study, conducted the field study, performed the behavioral and statistical analyses and prepared the manuscript, according to the advices of my supervisors. I am corresponding author of the manuscript.
ABSTRACT

Seasonal changes may have a strong effect on the safety of sleeping sites in arboreal primates. For example, changes in vegetation thickness may impact predation risk and energy expenditure related to thermoregulation. We investigated how seasonality influenced sleeping site characteristics and usage pattern in an arboreal primate living in a highly seasonal environment. The western woolly lemur (*Avahi occidentalis*) lives in the dry deciduous forest of north-western Madagascar where leaf coverage greatly varies across the year. We examined the hypothesis that these lemurs change their sleeping site behavior dependent on season. We collected data on sleeping site height and location, and characterized usage patterns in 6 radio-tagged pairs between May and December 2008. During the late dry season, pairs preferentially slept in the middle part of a tree. In contrast, there was no height preference during the early rainy season. The lemurs used more sleeping sites during the early rainy than during the late dry season and stayed more days at the same sleeping tree in the late dry season. Our findings support the hypothesis that season affects sleeping site selection in an arboreal primate species living in a highly seasonal environment. During the late dry season, western woolly lemurs are particularly conspicuous to hunters and we therefore suggest a better monitoring of the forest in this season to guarantee their future survival.
CHAPTER 3

PEACEFUL PRIMATES: AFFILIATION, AGGRESSION AND THE QUESTION OF FEMALE DOMINANCE IN A NOCTURNAL PAIR-LIVING LEMUR (Avahi occidentalis).


DOI 10.1002/ajp.20998

Contribution to the work

I participated in the design of the study, conducted the field study, performed the behavioral and statistical analyses and prepared the manuscript, according to the advices of my supervisors. I am corresponding author of the manuscript.
ABSTRACT

Affiliation / agonism and social dominance are central factors determining social organization in primates. The aim of our study is to investigate and describe, for the first time, the intersexual relations in a nocturnal and cohesive pair-living prosimian primate, the western woolly lemur (*Avahi occidentalis*), and to determine to what extent phylogeny, activity mode, or the cohesiveness of pair partners shape the quality of social interactions. Six pairs of western woolly lemurs were radio collared in the dry deciduous forest of northwestern Madagascar. Over 874 hours of focal animal sampling were conducted. All occurrences of social interactions involving a focal animal were recorded. The rate of affiliation between pair partners was significantly higher than the rate of agonism. Western woolly lemur pairs’ interactions were extremely peaceful. All decided agonistic conflicts (N=15) were exclusively initiated and won by the female. No female showed spontaneous submission towards her male partner. These results are in line with those of diurnal cohesive pair-living anthropoid primates. Findings support the hypothesis that social relations in pair-living primates are linked to the cohesiveness of pair partners in time and space irrespective of phylogeny and activity mode.
CHAPTER 4

THE ROLE OF ACOUSTIC SIGNALLING FOR SPACING AND COHESIVENESS IN A NOCTURNAL, COHESIVE PAIR LIVING LEMUR.

Ramanankirahina R., Joly M., Scheumann M., Zimmermann E. In preparation for publication.

Contribution to the work

I participated in the design of the study, conducted the field study, performed the behavioral, acoustic, and statistical analyses and prepared the manuscript, according to the advices of my supervisors. I will be corresponding author of the manuscript.
ABSTRACT

How social groups govern their distribution in time and space and maintain group cohesiveness is a central question in socioecology. For diurnal primates, living in dense forest environments with limited visibility, acoustic communication is known to represent an efficient mechanism, whereas its importance for nocturnal permanently pair-living primates is unknown so far. The aim of this study is to explore, for the first time, the role of acoustic signaling for spacing and cohesiveness in a nocturnal, arboreal, pair-living primate, taking the woolly lemur (*Avahi occidentalis*) living in Malagasy dry deciduous forest as model. Six males and six females belonging to six pairs were radio-collared and their activity and vocalizations and call-associated behavior were recorded using GPS-based focal animal sampling. By applying bioacoustic techniques, we identified three acoustically distinct and frequently used call types: the ava-hee call, the whistle call, and the growling call. The ava-hee call is a loud, two syllable call, given primarily at feeding sites, in the vicinity of home range boundaries. It often induces ava-hee calling in neighboring groups, but not in pair partners, suggesting that this call type signals territory ownership and governs spacing between pairs. The whistle call is a loud, harmonic call, not linked to feeding sites or home range boundaries. It is given primarily during locomotion when the caller is becoming visually isolated from the pair partner. It may evoke counter-calling between pair partners, but not with non-pair partners, supporting the function of pair cohesion. The growling call is a soft and noisy call consisting of rapidly repeated short broadband pulses. It is produced primarily at feeding trees and in response to approaching conspecifics or other species such as a sportive lemur or brown lemur. It is most likely a threatening call. Findings provide first empirical evidence in nocturnal, arboreal, permanently pair-living primates, showing that vocal signaling represents an important mechanism to regulate the distribution of pairs in space and govern intra-pair cohesion.
INTRODUCTION

A major question in socio-ecology is how social groups govern their distribution in time and space and maintain group cohesiveness (Boinski and Garber 2000; Couzin and Krause 2003; de Waal and Tyack 2003, Jacobs 2010; King and Sueur 2011). Anthropoid primates (except the orang-utan) and diurnal Malagasy lemurs live in permanent social groups in which group members cooperate in foraging, predator detection and defense, offspring rearing or resource defence by using elaborate sets of visual, tactile, olfactory and auditory signals for social communication (Cheney & Seyfarth 1977; Zimmermann 1992; Hauser 1996; Braune et al. 2005; Clarke et al. 2012). Whereas loud calls, high amplitude sounds with energy concentrated at low frequencies enhancing transmission in forest environments (Marten and Maler 1977; Waser and Waser 1977; Waser and Brown 1984), choruses (Hall and DeVore 1965; Tenaza 1976; Geissmann and Mutschler 2006) and song (Pollock 1986; Cowlishaw 1992; Geissmann and Mutschler 2006) are often used for inter-group spacing and group reunion, soft vocalizations are given to regulate intra-group cohesion and coordination (e.g. African elephants: Poole et al. 1988; Golden brown mouse lemur: Braune et al. 2005; Black howler monkeys: da Cunha and Byrne 2006; Spider monkeys: Ramos-Fernández 2008; Spehar and Di Fiore 2013).

In contrast to diurnal primates, nocturnal Malagasy lemurs live in highly diverse social systems (e.g. Müller and Thalmann 2000), making them to an ideal model group for understanding the evolution of mechanisms regulating intergroup spacing and group coordination in primates (Braune et al. 2005). Nocturnal, small-bodied and omnivorous lemurs, e.g. mouse lemurs, which form permanent sleeping groups, but forage solitarily during the night, use olfactory mechanisms to regulate the distribution of groups in space (Braune et al. 2005) and avoid predators (Sündermann et al. 2008; Kappel et al. 2011). Acoustic signals are used to govern mating, intra-group cohesion (mother-infant, sleeping group reunions) and group coordination (Hafen et al. 1998; Braune et al. 2005; Scheumann et al. 2007), as well as conflicts and conflict resolution with con- and heterospecifics (Zimmermann 2009). Nocturnal medium-bodied and folivorous lemurs, in which pair partners sleep permanently together but range apart from each other, e.g. sportive lemurs, use a broad variety of different loud call types or gouging for regulating space use and cohesiveness between pair partners and neighbors (e.g. Rasoloharijaona et al. 2006, 2010; Méndez-Cárdenas and Zimmermann 2009). Acoustic signals in these socially dispersed-living lemurs
express specific emotions and convey species-, group- and individual identity (e.g. Braune et al. 2005, 2008; Rasoloharijaona et al. 2006; Scheumann et al. 2007; Zimmermann 2009). Empirical bioacoustic studies in nocturnal permanently pair-living primates, helping to understand the evolution of mechanisms governing the distribution of primate groups in time and space are lacking so far.

Western woolly lemurs (*Avahi occidentalis*) are distributed in the dry deciduous forests of northwestern Madagascar and represent an excellent model for such an approach. These weasel-sized, medium-bodied lemurs form permanent pairs in which pair partners forage together during the night and sleep together in trees with dense foliage during the day (Albignac 1981; Warren and Crompton 1997; Ramanankirahina et al. 2012). As do sportive lemurs, woolly lemurs belong to the so-called clingers and leapers (Warren 1997; Warren and Crompton 1997), and are able to move rapidly through dense forests. In contrast to sportive lemurs, woolly lemurs are folivorous specialists, selecting underrepresented food resources (Thalmann 2001). The sexes are monomorphic and do not differ in body mass and size (Ramanankirahina et al. 2011). Pair partners interact extremely peacefully, however, though females are dominant in the feeding context (Ramanankirahina et al. 2011). The mean home range size of pairs was estimated to be about 1.59ha (Warren and Crompton 1997). Woolly lemurs are the only nocturnal representative of the family of Indriidae. Information on their vocalizations is limited so far. Petter and Charles-Dominiques (1979) were the first and only authors displaying spectrographic representations of the calls. However, they did not provide empirical information on the callers, call usage and context, nor on the geographical origin of the callers (Table 6). Harcourt (1991), Warren and Crompton (1997), and Thalmann (2003), studying feeding ecology, locomotion energetics and social behavior of woolly lemurs mentioned onomatopoetically described calls, the ava-hee call, the whistle call and the growling call, and speculated on their function (Table 6), but did not give empirical data linking acoustic structure to function.
Table 1: Presumed function of the ava-hee, whistle, and growling calls reported by Petter and Charles-Dominique (1979), Harcourt (1991), and Warren and Crompton (1997).

<table>
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</thead>
<tbody>
<tr>
<td>Presumed function</td>
<td>Species</td>
<td>Presumed function</td>
</tr>
<tr>
<td>Ava-hee call</td>
<td>Alarm vocalization</td>
<td><em>Avahi</em></td>
</tr>
<tr>
<td></td>
<td>Cohesion call</td>
<td><em>laniger</em></td>
</tr>
<tr>
<td>Whistle call</td>
<td>Distant communication calls</td>
<td><em>Avahi</em></td>
</tr>
<tr>
<td></td>
<td>Territorial signals</td>
<td><em>laniger</em></td>
</tr>
<tr>
<td>Growling call</td>
<td>Alarm calls</td>
<td><em>Avahi</em></td>
</tr>
<tr>
<td></td>
<td></td>
<td><em>laniger</em></td>
</tr>
</tbody>
</table>
The aim of the present study was therefore to explore for the first time to which extent acoustic signaling is used for governing spacing and cohesiveness in nocturnal, permanently pair-living primates, taking the western woolly lemur as a model. Based on previous knowledge, three hypotheses were put forth. 1. Since feeding and sleeping sites have been described as potential limited resource for woolly lemurs (Thalmann 2001, Ramanankirahina et al. 2012), we expected competition for them by means of vocal demarcation. We hypothesized therefore that auditory signals act as territorial displays governing the distribution of pairs in space. Our predictions were: The acoustic structure of potential vocalizations guarantees optimal transmission over larger distances in dense deciduous forest environment. Calling activity is higher at resource than non-resource sites. Acoustic signals will be produced primarily at the border of the home ranges, not in the core, to optimize transmission, and to minimize energy-consuming direct physical conflicts. Sexes show an asymmetric display activity higher in males than females since males will support females in saving energy investment in offspring. Calling induces counter-calling with the same call type in other pairs, but not in pair partners. 2. Woolly lemurs are known to forage in pairs or as family groups (Thalmann 2001, 2003) in a complex and dense three-dimensional forest environment. Thus we expected that pair partners maintain cohesion by means of calling, as shown for diurnal pair-living primates (e.g. Fan et al. 2009). Our predictions were: the respective vocalization will display an acoustic structure that guarantees optimal transmission over larger distances in dense deciduous forest environments. Calling activity is not different between resource and non-resource sites. It will be linked to locomotion. Males and females do not show a significant difference in calling rate. Calling will induce counter-calling with the same call type in the pair partner, but not in neighbors. 3. Woolly lemurs were reported to live sympatrically with other primates and compete for limited resources (Warren and Crompton 1997; Thalmann 2001). Our third hypothesis was therefore that calling threatens con- and/or heterospecifics, minimizing the risk of direct physical combat. We predicted that calling activity is linked to feeding sites, and related to feeding context. Males and females do not show a significant difference in calling rate. Calling will induce withdrawal, counter-calling with the same call type in conspecifics or physical combat in con- or heterospecifics.
METHODS

1. Study area and animals

The study was carried out in the research area JBA (Jardin Botanique A, 30.6 ha) of the Ankarafantsika National Park in northwestern Madagascar. The vegetation consists of dry deciduous forests, characteristic of the western lowlands of Madagascar. Six pairs of western woolly lemurs were captured: six adult males and six adult females. Each animal was fitted with a radiotransmitter on a backpack (for more details on methods, see Ramanankirahina et al. 2012).

2. Data collection

GPS-based radio telemetry was used to monitor activity, and habitat usage of western woolly lemurs. Using a portable receiver and antenna, each radio-collared individual was followed for eight months, from May to December 2008. All radiocollared individuals were observed with the aid of headlamps during two half nights (6-12 p.m. and 12-6 a.m.) every month except for May and August (one half night 6-12 p.m.). The total contact time was 874 hours (Ramanankirahina et al. 2011). Focal animal sampling with continuous recording was conducted (Altmann 1974, Martin & Bateson 1993). The movement of a focal animal was noted by taking the geographical positions at every new position. Calls were classified onomatopoetically into three major call types: ava-hee call, whistle call and growling call. Information about the identity of the caller, the time, the type of the tree where the focal individual vocalized (resource site=site used for feeding or sleeping, or non-resource site=all other sites, except feeding/sleeping sites), and the behavioural context (resting: lies horizontally or vertically on a branch or sites, sometimes closes the eyes; feeding: eats leaves, or fruits.; locomotion: climbs up or down a tree or leaps to another tree) according to Méndez-Cárdenas & Zimmermann (2009) as well as events inducing a call were recorded. If a call was immediately responded to by another individual, the identity of the responder (pair partner or other (neighbor, or stranger group) was noted as well as the type of response.
3. Acoustic recording and analyses

Vocalizations of the focal animal were recorded with a stereo cassette recorder (Sony Professional WM-D6C) onto audio recording cassettes (Sony super chrome class UX-S IECII/Type II), using a Sennheiser directional microphone (K6 power module and ME67 recording head) with a windshield. All recordings were transferred and digitized at 16 bits, 44.1 kHz, using Batsound Pro 3.31 (FFT 512, Hanning window). Spectrograms of acoustic recordings were visually inspected.

In total 733 vocalizations of three major call types were recorded and termed onomatopoeically as the ava-hee call, the whistle call, and the growling call (Figure 10). For acoustic characterization of call types, high quality recordings were selected (calls not disturbed by background noise, such as other animals calling, >7dB higher than background noise). In total, 291 high quality calls were used for the acoustic analysis (74 ava-hee calls, 146 whistle calls, and 71 growling calls) by Signal 4.1 (Kim Beeman, Engineering design). To describe the acoustic structure of vocalizations, 11 temporal and 8 spectral parameters were measured (Table 7). For descriptive analysis, the mean and standard deviation of each parameter per call type were calculated.
Figure 5: Sonagrams of the three most frequently emitted call types by six pairs of western woolly lemurs: (a) ava-hee call, (b) whistle call, (c) growling call.
Table 2: Description of the acoustic parameters measured from ava-hee (a), whistle (b) and growling (c) calls.

<table>
<thead>
<tr>
<th>Spectral parameters measured</th>
<th>Calls</th>
<th>Temporal parameters measured</th>
<th>Calls</th>
</tr>
</thead>
<tbody>
<tr>
<td>Peak frequency (Hz)</td>
<td>Peak</td>
<td>Duration of a call (ms)</td>
<td>Durt</td>
</tr>
<tr>
<td>Peak frequency of the first syllable (Hz)</td>
<td>Peak 1</td>
<td>Duration of the first syllable (ms)</td>
<td>Durt 1</td>
</tr>
<tr>
<td>Fundamental frequency (Hz)</td>
<td>Fo</td>
<td>Duration of the second syllable (ms)</td>
<td>Durt 2</td>
</tr>
<tr>
<td>Minimum fundamental frequency (Hz)</td>
<td>Fo min</td>
<td>Duration of inter-syllable interval (ms)</td>
<td>Inter</td>
</tr>
<tr>
<td>Maximum fundamental frequency (Hz)</td>
<td>Fo max</td>
<td>Duration of inter pulse 1 and pulse 2 (ms)</td>
<td>Inter 1</td>
</tr>
<tr>
<td>Fundamental frequency of the first syllable (Hz)</td>
<td>Fo 1</td>
<td>Duration of inter pulse 2 and pulse 3 (ms)</td>
<td>Inter 2</td>
</tr>
<tr>
<td>Minimum fundamental frequency of the first syllable (Hz)</td>
<td>Fo min 1</td>
<td>Duration of inter pulse 3 and pulse 4 (ms)</td>
<td>Inter 3</td>
</tr>
<tr>
<td>Maximum fundamental frequency of the first syllable (Hz)</td>
<td>Fo max 1</td>
<td>Duration of inter pulse 4 and pulse 5 (ms)</td>
<td>Inter 4</td>
</tr>
<tr>
<td>Peak frequency of the second syllable (Hz)</td>
<td>Peak 2</td>
<td>Duration of the first pulse (ms)</td>
<td>Dur 1</td>
</tr>
<tr>
<td>Fundamental frequency of the second syllable (Hz)</td>
<td>Fo 2</td>
<td>Duration of the second pulse (ms)</td>
<td>Dur 2</td>
</tr>
<tr>
<td>Minimum fundamental frequency of second syllable (Hz)</td>
<td>Fo min 2</td>
<td>Duration of the third pulse (ms)</td>
<td>Dur 3</td>
</tr>
<tr>
<td>Maximum fundamental frequency of second syllable (Hz)</td>
<td>Fo max 2</td>
<td>Duration of the fourth pulse (ms)</td>
<td>Dur 4</td>
</tr>
</tbody>
</table>

Temporal parameters calculated

<table>
<thead>
<tr>
<th>Number of pulse</th>
<th>No Pulse</th>
<th>c</th>
</tr>
</thead>
</table>
4. Analysis of call-associated behaviors

For the analysis of calling rates, calls given within a 1mn interval were counted as one event. For each call type, the number of calling events for each individual per night was counted and divided by the total contact time per night per individual. Calling rates between sexes were compared by performing Mann-Whitney U Test. The calling rate for each call type per pair was also calculated.

For each call type and individual, the number of calling events produced at the two site categories was counted and divided by the total number of calling events per individual. A Wilcoxon Matched Pairs Test was used to test for statistical differences between site categories.

For each call type and individual, the number of calling events related to three behavioral contexts were scored and divided by the total number of calling events per individual. A Friedman ANOVA was applied to examine whether there was a significant effect of behavioral context on the respective call type. If a significant effect appeared, Wilcoxon Matched Pairs Test was applied.

For each calling event of a call type of an individual, it was scored whether and how it was responded to. The total numbers of events were then counted.

5. Determination of home range size and overlapping area

All GPS coordinates were entered into ArcView GIS 3.3 (ESRI) to calculate home range size (Ganas & Robbins 2005, Harris 2006). Home range size was determined by using all the GPS positions (Male: median, 532 points/individual, range 427-661 points, N=6; Female: median, 503 points/individual, range 186-645 points, N=6) collected during the nocturnal focal animal sampling across the whole period. Calculations were based on more than 180 GPS points/individual. To be comparable with most other lemur studies, we estimated home range sizes and overlaps by using the 100% Minimum Convex Polygon (MCP). We used the 95% and 50% Fixed Kernel method (Hayne 1949, Worton 1989) to differentiate core and border of home ranges and to link them to calling activity. To determine if there was a sex difference in home range size, the home range sizes of males and females were compared using the Mann-Whitney U Test. Additionally, the proportions of home range overlaps between the different focal individuals were calculated by an overlay procedure of
the geoprocessing extension in ArcView 3.3. Mann-Whitney U Test was used to test if there was a significant difference in the proportion of overlapping area between neighboring male/male and female/female and between pair partner.

6. Spatial distribution of the calling positions

The calling position of the three call types of each pair was overlaid with the home range by using ArcView GIS 3.3 to explore if calls were emitted at the periphery or non-periphery of the home ranges. We defined the non-periphery area as the core area of the home range (see Laver and Kelly 2008) and the periphery as the border of the home range. To define the border and core area of the home ranges, the 95% and 50% fixed kernels contours were used. Each contour represents the probability that the pair was found in the specified area within the study period (Horner & Powell 1990). The median core area for each pair was calculated. From the geoprocessing extension in ArcView 3.3, the numbers of calls emitted in the core area and in the periphery area were quantified for each pair.

RESULTS

1. Acoustic characteristics of call types

The three call types, which occurred most frequently, were the ava-hee call, the whistle call, and the growling call (Figure 10).

The ava-hee call (N=8, n=74; Figure 10a, Table 8) represents a loud, partly noisy, broadband call. It contains two syllables with a peak frequency of 996 ± 114 Hz and 3876 ± 170 Hz respectively. The total duration of the ava-hee call is 366 ± 9 ms, with the duration of 107 ± 2 ms, respectively for the first syllable and 229 ± 8 ms for the second syllable.

The whistle call (N=12, n=146; Figure 10b, Table 8) is a loud, harmonic call. It is given as a single call or as a call series. The peak frequency is 2730 ± 152 Hz. The call lasts 1280 ± 36 ms.

The growling call (N=8, n=71; Figure 10c, Table 8) is a soft and noisy call consisting of rapidly repeated short broadband pulses. The peak frequency is about 4339 ± 234 Hz. The call lasts 1017 ± 37 ms. The whistle call is the longest call of all measured call types, followed by the growling and ava-hee call.
Table 1: Acoustic parameters of the avahee call, the whistle call and the growling call.

<table>
<thead>
<tr>
<th>Call type</th>
<th>Ava-heel</th>
<th>Whistle</th>
<th>Growling</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number of animal (N)</td>
<td>8</td>
<td>12</td>
<td>8</td>
</tr>
<tr>
<td>Number of calls (n)</td>
<td>74</td>
<td>146</td>
<td>71</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Spectral parameters measured</th>
<th>Ava-heel</th>
<th>Whistle</th>
<th>Growling</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean</td>
<td>SD</td>
<td>Mean</td>
<td>SD</td>
</tr>
<tr>
<td>Peak</td>
<td>2730.02</td>
<td>151.884</td>
<td>4338.79</td>
</tr>
<tr>
<td>Peak 1</td>
<td>995.88</td>
<td>113.788</td>
<td>-</td>
</tr>
<tr>
<td>Fo</td>
<td>4377.32</td>
<td>21.151</td>
<td>-</td>
</tr>
<tr>
<td>Fo min</td>
<td>4098.15</td>
<td>21.714</td>
<td>-</td>
</tr>
<tr>
<td>Fo max</td>
<td>4659.52</td>
<td>21.3</td>
<td>-</td>
</tr>
<tr>
<td>Fo 1</td>
<td>688.26</td>
<td>17.545</td>
<td>-</td>
</tr>
<tr>
<td>Fo min 1</td>
<td>415.70</td>
<td>18.031</td>
<td>-</td>
</tr>
<tr>
<td>Fo max 1</td>
<td>899.93</td>
<td>20.422</td>
<td>-</td>
</tr>
<tr>
<td>Peak 2</td>
<td>3876.36</td>
<td>170.176</td>
<td>-</td>
</tr>
<tr>
<td>Fo 2</td>
<td>4255.03</td>
<td>53.3</td>
<td>-</td>
</tr>
<tr>
<td>Fo min 2</td>
<td>3944.92</td>
<td>46.991</td>
<td>-</td>
</tr>
<tr>
<td>Fo max 2</td>
<td>4499.16</td>
<td>57.957</td>
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<table>
<thead>
<tr>
<th>Temporal parameters measured</th>
<th>Ava-heel</th>
<th>Whistle</th>
<th>Growling</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean</td>
<td>SD</td>
<td>Mean</td>
<td>SD</td>
</tr>
<tr>
<td>Durt</td>
<td>365.5</td>
<td>8.921</td>
<td>1280.08</td>
</tr>
<tr>
<td>Durt 1</td>
<td>106.96</td>
<td>2.098</td>
<td>-</td>
</tr>
<tr>
<td>Durt 2</td>
<td>229.24</td>
<td>7.967</td>
<td>-</td>
</tr>
<tr>
<td>Inter</td>
<td>29.30</td>
<td>2.412</td>
<td>-</td>
</tr>
<tr>
<td>Inter 1</td>
<td>-</td>
<td>-</td>
<td>-</td>
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<tr>
<td>Inter 2</td>
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<td>Inter 3</td>
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<tr>
<td>Inter 4</td>
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<td>-</td>
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<tr>
<td>Dur 1</td>
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<tr>
<td>Dur 2</td>
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<td>Dur 3</td>
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<td>Dur 4</td>
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<tr>
<td>Dur 5</td>
<td>-</td>
<td>-</td>
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<table>
<thead>
<tr>
<th>Temporal parameters calculated</th>
<th>Ava-heel</th>
<th>Whistle</th>
<th>Growling</th>
</tr>
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<tbody>
<tr>
<td>Mean</td>
<td>SD</td>
<td>Mean</td>
<td>SD</td>
</tr>
<tr>
<td>No Pulse</td>
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</tr>
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</table>
2. **Calling rates of the respective call types**

The ava-hee call was produced with the median rate of 0.05/h (range 0 - 0.15/h, N=5) by males and 0.08/h (range 0.01 - 0.48/h N=6) by females. The median rate of the whistle call was 0.36/h (range 0.15 - 0.47/h N=6) by males and 0.14/h (range 0.1 - 0.35/h N=6) by females. The growling call was emitted with the median rate of 0.53/h (range 0.22 - 1.57/h N=6) by males and 0.61/h (range 0.32 - 2.21/h N=6) by females. Sexes showed no significant difference in calling rate for each call type (Mann-Whitney U Test, ava-hee: Nmale=5 Nfemale=6 U=12 p=0.34, whistle: Nmale=6 Nfemale=6 U=6 p=0.06, growling; Nmale=6 Nfemale=6 U=16 p=0.75). Growling and whistle calls were the most commonly used vocalizations in the repertoire, with the rate of call of 0.69/h (Median, range 0.357 – 1.626/h) and 0.269/h (Median, range 0.205 – 0.456/h) respectively per pair. The rate of ava-hee call was 0.08/h (Median, range 0.024 – 0.239/h) per pair.

3. **Call-associated behaviour and context**

A total of 75 ava-hee call events were found in 11 focal animals. Calls were given significantly more often at a resource sites than a non-resource sites (Wilcoxon Matched Pair Test: Resource/Non-resource sites N=11 Z=2.8 p=0.005). The ava-hee call was produced during locomotion, feeding and resting, with no difference between the three context categories (Friedman test N=11 X²=3.2 df=2 p=0.21, Figure 11). 21 of 75 ava-hee call events were spontaneous and evoked no vocal response. 22 were responded to by another group with a similar call. 28 were responses to an ava-hee call emitted by another group call.
The 199 whistle call events were not given significantly more often at a resource than a non-resource site (Wilcoxon Matched Pair Test: Resource/Non-resource sites N=12 Z=1.51 p=0.13). The whistle call occurred more frequently in the locomotion context than in the two other contexts (Friedman test N=12 X²=17.7 df=2 p=0.0001, Wilcoxon Matched Pair Test: Feeding/Resting N=12 Z=0.46 p=0.65, Feeding/Locomotion N=12 Z=2.9 p=0.003, Resting/Locomotion N=12 Z=3.1 p=0.002, Figure 11). Most whistle call events (148 of 199) occurred spontaneously and yielded no vocal response. 26 were replied by pair partners by the whistle (14) or growling call (12). 25 of whistle call events were responses to a whistle call from the pair partner. The whistle call was frequently given when the pair partners were apart from each other (133 of 199 whistle call events). Afterwards, the pair partners synchronized activity.
A total of 501 growling call events occurred. Growling call activity was higher at a resource than a non-resource site (Wilcoxon Matched Pair Test: Resource/Non-resource sites N=12 Z=2.35 p=0.02). Growling calls were associated more frequently with the feeding context than with the two other contexts (Friedman test N=6 X²=9.5 df=2 p=0.009, Wilcoxon Matched Pair Test: Feeding/Resting N=12 Z=2.82 p=0.005, Feeding/Locomotion N=12 Z=2.4 p=0.02, Resting/Locomotion N=12 Z=1.2 p=0.24, Figure 11). The majority of growling calls (416 of 501) were given spontaneously. 69 were produced in response to a whistle call from a pair partner, and 16 to the presence of other species (11) or other conspecifics (5).

Sometimes the caller gave an ava-hee (n=4) and/or growling (n=5) call as a response to a conspecific intruder. Only growling calls (n=11) were given to the presence of heterospecific intruders such as *Lepilemur edwardsi*, *Eulemur fulvus* and a bird. *Avahi* stopped calling when the intruder withdrew.

### 4. Home range size and overlapping area

Using the MCP, the male median home range size was 1.94 ha (range 1.14-3.08ha) and female median home range size was 1.65ha (range 1.16-3.09ha). Males overlapped more with home ranges of their male neighbors, than females did with female neighbors (Male, median 23%, range 12%-46%; Female, median 8%, range 4%-15%; Mann-Whitney Test, Nmale=5 Nfemale=5, U=1 p=0.016, Figure 12). Males overlapped with female neighbors on 13% (Median, range 10% - 22%) of their total home range. Females overlapped with male neighbors on 11% (Median, range 9% - 44%) of their total home range. Home ranges of pair partners overlapped strongly (Male, median 84%, range 64%-95%; Female, median 93%, range 91%-100%, Figure 12). No significant differences were observed in the overlapping area of male and female pair partners (Mann-Whitney U Test Nmale=6 Nfemale=6, U=7 p=0.08). We did not find any significant differences between home ranges of males and females (Mann-Whitney U Test, Nmale=6 Nfemale=6, U=13 p=0.42). The median home range size of pairs was 2.03ha (range, 1.2 – 3.3ha). Home ranges of pairs overlapped about 26% (Median, range: 15% - 47%) with those of neighboring pairs.
Figure 7: Home ranges of the twelve individuals of western woolly lemurs (Male with bold line and female with simple line) with MCP.
We did not find any differences between the sexes. Consequently, the spatial distribution of the calling positions was based on the home ranges and calling activity of pairs.

5. Spatial distribution of the calls

Using the 95% Kernel, the median home range size of pairs was 1.84ha (range, 1.3 – 3.21ha, Figure 13). Home ranges of pairs overlapped with those of their neighbors by about 21% (Median, range: 11% - 33%) of the total home range. The median core area of pairs were 0.25ha (range 0.2 – 0.4ha) using the kernel at 50%. No overlapping of core area existed between neighboring pairs or neighboring individuals.
Figure 8: Home ranges of the six pairs of western woolly lemurs with Kernel.
Mapping the ava-hee calling locations revealed that 72% occurred outside the core area of the respective pairs. Caller positions seem to be more often in the border area than in the core area (Figure 14). However, they were dispersed across the home range area for the whistle (Figure 15) and growling call (Figure 16).

![Map of Ava-hee calls](image)

**Figure 9:** Distribution of the ava-hee calls in the home range of the six pairs
**Figure 10:** Distribution of the whistle calls in the home range of the six pairs
Figure 11: Distribution of the growling calls in the home range of the six pairs
DISCUSSION

Our study revealed that acoustic signaling was used as a mechanism to govern pair cohesion and inter-pair spacing in a nocturnal, pair-living primate, the woolly lemur. Call structure and usage of the reported three call types provided the first empirical evidence for their functions. Findings will be discussed regarding the hypotheses and predictions postulated in the introduction. Furthermore we will compare findings with those of other members of the same family, the Indriidae to illuminate commonalities and species-specific adaptations in vocal communication.

1. Vocalizations of woolly lemurs and their potential functions

In our study we acoustically characterized three most common vocalizations of the western woolly lemur, the ava-hee call, the whistle call and the growling call, with regard to their acoustic structure and usage to deduce their function.

Two call types, the ava-hee call and the whistle call, are given with high amplitude and display energy concentrated at low frequencies. These acoustic characteristics are known to minimize degradation and attenuation by high ambient noise and maximize sound transmission and localization over longer distances (Marten and Maler 1977; Waser and Waser 1977, Waser and Brown 1984), making callers more distinctive at the species, sex and individual level. These two call types can thus be considered as loud calls. In contrast, the growling call has a fairly low amplitude with call attributes that are recognizable only at short distances. In fact, this call type was only produced at short distances when the caller and receiver maintained visual contact.

Western woolly lemurs base their diet on rare and underrepresented resources (Thalmann 2001) and are known to have a limited number of high quality sleeping sites, in particular during the dry season (Ramanankirahina et al. 2012). If resources are rare, competition for them may arise either by costly direct physical combat or by indirect means such as olfactory or vocal demarcation (e.g Mert-Millhollen 1979; Petter and Charles-Dominiques 1979; Schilling 1980; Raemaekers and Raemaekers 1985; Kinnaird 1992; Miller et al. 2003; Geissmann and Mutschler 2006). As predicted in hypothesis 1, western woolly lemurs use the ava-hee call as a loud call to advertise territory ownership and to space
strangers and neighbors. We found that calling activity was higher at resource than non-resource sites and that calls were produced primarily at the border of the home ranges, not in the core. Calling induces counter-calling with the same call type in other pairs, but not in pair partners. In contrast to our prediction, the sexes did not show an asymmetric display of activity with activity being higher in males than females. This means, males do not call to support females in saving energy for other beneficial purpose such as investment in offspring. However, they might use another mechanism to defend resources for increasing female reproductive fitness, like chemical signals. In mammals, scent-marking has been used to identify food resources (e.g. Kruuk 1992), or to mark the territory (e.g. Roberts and Dunbar 2000).

Woolly lemurs forage in pairs or as family groups in a complex three-dimensional forest environment. The visual contact between pair partners is often interrupted when animals are traveling in dense forests. Keeping contact between the pair partners is thus of primordial importance. As predicted in hypothesis 2, western woolly lemurs use whistle calls to maintain pair cohesion. Calling activity is linked to the locomotion context, and not different between resource and non-resource sites. Males and females do not show a significant difference in calling rate. Calling induces counter-calling with the same call type in the pair partner, but not in neighbors. Calls used to maintain cohesion and coordinate movements between group members are known from a lot of diurnal primates (e.g. Kinzey et al. 1977; Mitani 1985; Estes 1991; Boinski and Garber 2000; Geissmann and Orgeldinger 2000; Fan et al. 2009).

Western woolly lemurs live sympatrically with other primates and are suggested to compete for limited resources. As predicted in hypothesis 3, western woolly lemurs produce a growling call to threaten con- and/or heterospecifics, minimizing the risk of direct physical combat. Calling activity is linked to feeding sites, and related to feeding context. Males and females do not show a significant difference in calling rate. Calling induces withdrawal of heterospecifics and conspecifics. By calling, western woolly lemurs may reduce the costs of possible confrontation with potential competitors, and avoid costly injuries.

2. Comparison of social calls within the Indriidae

Do western woolly lemurs show the same pattern of vocal behavior as their relatives of the family Indriidae? Sifaka vocalizations seem to be more varied than those of woolly
lemurs. For example silky sifakas (*Propithecus candidus*) showed a high vocal activity with 7 calls per hour per individual and have a vocal repertoire size of about 7 call types (Patel et al. 2005) which they use for aerial disturbance, submissive signal, lost call, contact call, low level threat vocalization, and alarm call. Indris are also known as highly vocal, using songs or duets for territory advertisement and 8 other call types for anti-predator defense, maintaining contact, issuing a warning signal, a call associated with physical aggression, and a contact seeking call (Petter and Charles-Dominique 1979; Maretti et al. 2010). Sifakas and indris are reported to use soft vocalizations to remain in contact with other group members, thus they are considered to be group-cohesion calls (Petter and Charles-Dominique 1979), functionally similar to the whistle calls in woolly lemurs. Sifakas use chorusing (simultaneous calling of all group members) and Indris song with a complex temporal pattern for territory demarcation and loud alarm calls for advertising the detection of disturbances or predators (Maretti et al. 2010; Fichtel and Kappeler 2011). Woolly lemurs also demarcate their territory vocally. However, it is only one pair partner which vocalizes. The acoustic structure of the ava-hee call is also not as temporally complex as the functionally homologous calls in the other two groups. During our study period, we furthermore never observed a woolly lemur-predator interaction and thus never recorded any alarm calls.

3. Conclusions and areas for future research

All in all, this study provides first empirical and quantitative information on the role of acoustic communication for spacing and cohesiveness in the woolly lemur as a representative of the nocturnal pair-living primates. As in their diurnal relatives, acoustic signaling represents an important mechanism to regulate distances between pairs in space and to maintain cohesion between pair partners. A more sophisticated acoustic analysis of the vocalizations of woolly lemurs and playback experiments are now urgently needed to explore to which extent woolly lemurs use and perceive the messages acoustically conveyed in their calls. Furthermore, as loud calls are often used successfully to assess taxonomic and phylogenetic relations or migrations patterns in other primates (Davila Ross and Geissmann 2007; Méndez-Cárdenas et al. 2008; Meyer et al. 2012), it would be interesting to examine the use of loud calls for conservation purposes in this endangered lemur species. Woolly lemurs are known to develop prominent scent glands under the chin (Warren and Crompton 1997).
Further investigations are thus needed to explore to which extent woolly lemurs use olfactory signalling for communication.

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Chapter 4

THE ROLE OF ACOUSTIC SIGNAL


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Chapter 4

THE ROLE OF ACOUSTIC SIGNAL


CHAPTER 5

GENERAL DISCUSSION
The study of sociality and communication is a major topic in behavioural ecology. It provides important insights into the interplay of the ecological determinants of sociality. Individuals live in social networks characterized by sleeping groups, interactions through vocalizations and/or scent-marking and occasional encounters at night (e.g. CHARLES-DOMINIQUE 1977, 1978; BEARDER 1987). Here, I will discuss the significance of sleeping site ecology for the conservation of primates, and woolly lemurs in particular. Furthermore I will compare my findings on sociality and communication with those on other related primate species to embed my findings on woolly lemurs into our current knowledge of the family Indriidae. Based on that, I will put forth perspectives for future research.

**Sleeping site ecology in primates and its significance for conservation**

In chapter 2, I have demonstrated that sleeping sites are a potentially limited resource for woolly lemurs, especially during the dry season, and that sleeping site ecology varies according to season. During the late dry season, woolly lemurs often reused the same sleeping site and preferred to sleep at the height of 5-10 m. My findings suggest that western woolly lemurs are particularly conspicuous for hunters during the dry season since they are at an accessible height for humans. They are uncovered, obvious to hunters, and can be picked up by hand without the need for weapons (GARCIA u. GOODMANN 2003). Habitat requirements of species may determine their vulnerability to anthropogenic disturbance. Many kinds of primates use nests, tree holes or hollows, and open vegetation for sleeping site (e.g. RADESPIEL et al. 1998, BEARDER et al. 2003, RADESPIEL et al. 2003, RASOLOHARIJAONA et al. 2003, SCHÜLKE AND KAPPELER 2003, RASOLOHARIJAONA et al. 2008, BIEBOUW et al. 2009). They require a special physical characteristic on their sleeping tree to allow them to stay safely during their long resting time. For example, arboreal primates sleeping in open vegetation tend to select trees with large diameters and large crown (e.g. VON HIPPEL, 1998; DI BITETTI et al. 2000; LI et al. 2006; CUI et al. 2006; FAN u. JIANG 2008; XIANG et al. 2010). Living in a harsh environment, monkeys preferred tall conifers at middle slopes (CUI et al. 2006). Information about the characteristics and usage of sleeping sites helps in conservation planning and the restoration of habitat (PLUMPTRE u. REYNOLDS 1997; BLOM et al. 2001; JOHNSON et al. 2004).

In defoliated trees, primates are easily detectable making the animal using the trees for concealment vulnerable to predators and hunters (PEETZ et al. 1992). Humans are among the
predators of animals. Many primate populations are severely threatened by human activities (WILSON u. WILSON 1975; HAMILTON et al. 1986; WHITE u. OATES 1999; COWLISHAW u. DUNBAR 2000). In the gray monkeys, for example, humans were likely the primary predators (Xiang et al. 2009). In a remote forest of western Brazilian Amazonia, more than 80 woolly monkeys, spider monkeys and howlers were killed by a single family of rubber tapers (Peres 1990). Hunting may have played a part in the extinction of some Malagasy lemurs (Perez et al. 2005). It may be more widespread than previously thought and deserves urgent attention from conservationists. Even though all lemur species are protected, participation in hunting of protected species is widespread. Around the world, hunting is the second most important threat to primate populations behind the loss of habitat (MITTERMEIER et al. 2006). It is a serious threat to long-term conservation and species survivorship. Thus, hunting and habitat destruction and degradation threaten the survival of many primate species (SANDERSON et al. 2002).

My data suggests that arboreal primates sleeping in open vegetation are easy to find and to catch in the dry season when trees are leafless. My findings have significant implications for forest management. Based on my results and analysis, I make the following management recommendations for the conservation of arboreal primates. We need to identify the characteristics of the sleeping trees potentially important for the arboreal species, for example large trees with dense coverage. Conservation management strategies should ensure the maintenance of these trees and suitable habitats necessary to the survival of the animals. Furthermore, the management of the reserve or park should monitor illegal poaching by increased patrolling and law enforcement, and carry out an education program involving conservation awareness to ensure that villagers do not kill the animals. Parks and reserves should maintain better monitoring of the forest, particularly during the dry season, to guarantee the future survival of the animals. Further research into sleeping tree availability should enable a better assessment of the conservation needs of these species. Indeed, there may well be other cues, not measured in my study, that are important for arboreal primates. The lack of information on habitat requirements of some arboreal primates precludes well-informed management decisions and further research is clearly required.

**Social systems and social relations within Indriidae**

Woolly lemurs are the only taxa among nocturnal strepsirrhines living in family groups (THALMANN 2001). In the family of Indriidae to which woolly lemurs belong, the
other taxa (*Propithecus, Indri*) live either as pairs, in small family groups or in multi-male multi-female systems. Living in pairs or small family groups may reduce mortality and increase foraging success. Food items as well as sleeping sites are patchily distributed for woolly lemurs, especially in the dry season (THALMANN 2001; RAMANANKIRAHINA et al. 2012). It might be therefore advantageous for both male and female woolly lemurs to share their range with a familiar mate to avoid predation and defend territories. Because predation results in death, selection to avoid it must be very strong. Moreover, males are unable to maintain territories that can support more than one female if females are so widely distributed in space. They have a small body size and low energy diet. They are forced into pair living as energy-saving strategy (NORSCIA u. BORGOGNINI-TARLI 2008). Furthermore, most folivorous mammals are diurnal, woolly lemurs are thus assigned to secondary nocturnal habits like in *Aotus*, the only nocturnal anthropoid (GANZHORN et al 1985; MARTIN 1990). The pressures of predators (Hawks and Eagles) are suggested to explain the nocturnal activity in *Aotus*. Thus, living-group may be the ancestral characteristic in woolly lemurs, retained from a diurnal activity pattern (GANZHORN et al 1985).

Despite its nocturnal activity, the western woolly lemurs show the same pattern of pair relations as their diurnal relatives living in either pairs or multi-male multi-female systems. Unambiguous female dominance (agonistic superiority of the female over males across different contexts) was reported for the diurnal species of the socially cohesive lemurs of the family Indriidae (POLLOCK 1979; MEYERS 1993; POCHRON et al. 2003). The degree of female dominance is variable among the lemurs and described to be affected by social system and activity pattern (RADESPIEL u. ZIMMERMANN 2001). Female dominance is a rare trait in social systems of mammals and within primates, but seems to be widespread among the lemurs of Madagascar (DUNHAM 2008). The direction of aggressive or submissive behaviours in agonistic encounters and the outcome of intersexual conflicts are frequent measures of dominance. In western woolly lemurs, affiliative behaviours are considerably more common than agonistic behaviours. Male and female partners interacted peacefully. Agonistic behaviour was rarely observed and always initiated by the female. According to the definition of dominance (RADESPIEL u. ZIMMERMANN 2001) females of the western woolly lemurs showed unambiguous dominance over males, meaning dominance across different contexts. Females won every decided intersexual conflict. Males exhibited submissive behaviours to their mates in the absence or presence of aggressive behaviour from females. Thus, female dominance is not linked to activity pattern and social system, but is an
ancestral trait originating from a common ancestor. In order to better understand the evolution of female dominance, more empirical and quantitative studies on the context, distribution and outcome of intersexual relationships are needed.

**Mechanisms regulating inter- and intra-pair spacing: acoustic communication**

Individuals interact physically and vocally. In chapter 4, I have demonstrated that western woolly lemurs depend on acoustic signalling to maintain contact and to manage intra- and inter-pair interaction. From my findings, *Avahi* produces loud calls for resource/territorial defence and aggregation of group. Mate defence or mate attraction did not appear to be the function of the loud calls in western woolly lemurs. The vocal rate of the loud calls did not increase during the dispersal or mating season. Male and female produced the long distance calls with the same rate, which is in contrast with the mate defence hypothesis suggesting that loud calls are more common in males than females. Males are thought to compete for mates while females compete mainly for resources (EMLEN u. ORING 1977; NUNN 1999).

The function of one loud call in woolly lemurs may be similar to the loud calls in *Indri*. Woolly lemurs emit ava-hee calls to communicate with neighbouring groups, to announce their presence within the territory, and to make information available about their location and distance. However, *Indri* use song or duets for territorial defence (THALMANN et al. 1993, GEISSMANN u. MUTSCHLER 2006). A duet was not found in my study of woolly lemurs. Patel (2010) does not record any call functioning for a territorial defence in their study on *Propithecus candidus*. However, PETTER u. CHARLES-DOMINIQUE (1979) reported that *Propithecus sp.* utter a barking call for distant communication between groups. They are often associated with territorial confrontations and evoke counter-calling from neighbouring groups. *Propithecus* are also reported to use scent-marking for territorial defence (e.g. POCHRON et al. 2005). Western woolly lemurs have marked trees during my follows but the functions of this behaviour remain unknown. This means that acoustic signals might not be linked to phylogenetics since *Indri, Propithecus* and *Avahi* show very different ways of communicating.

Western woolly lemurs ultimately remain spatially cohesive by means of calling. They use loud calls, whistles, to maintain and coordinate movements when they are separated. The loud calls seemed to serve as contact calls that maintained group cohesion and prevented individuals from becoming lost. In contrast, *Indris* use a low-pitched and low intensity
vocalization to maintain close contact with the group during resting activities or group displacements (MARETTI et al. 2010). Propithecus use low amplitude, tonal, and very low frequency contact calls during group movement and in a variety of circumstances such as affiliation, foraging and while resting (PATEL 2010). Indri and Propithecus use a short distance communication call to permit the animals to remain in contact during locomotion. Additionally, Propithecus possesses one call (howl) that they emit when individuals become spatially separated from the group which could act in the same way as the whistle call in Avahi. However, howl calls get always another type of call (Zzuss) in response from group members which is the same as the whistle call. Thus, it seems that western woolly lemurs do not show similar patterns of communication as their family relatives when remaining in contact with member of groups, confirming our statement above that acoustic signal might not be linked to phylogenetics.

In the presence of other species, western woolly lemurs produce the growling call, a soft and noisy call consisting of rapidly repeated, short, broadband pulses, used as a threatening call. This is a no predatory event. In Propithecus, they do emit purr call towards human observers, acting as low-level threat vocalization. In Indris, there is no similar vocalization but in response to disturbances, they reacted with calls of medium intensity (Kiss). In the presence of aerial predator, Indris emit a loud and harsh vocalization use as a standalone vocal signal. When terrestrial predators are present, they produce rhythmic, rapid alerting calls given in series of short, loud notes (MARETTI et al. 2010). Propithecus produce high-amplitude calls containing clear harmonic components in combination with substantial broadband noise (Zzuss) to terrestrial disturbances, and the roar call, a high amplitude broadband call to aerial disturbance (Patel 2010). The two diurnal Indriidaes give both different alarm calls for aerial and terrestrial predators (POLLOCK 1975; PETTER u. CHARLES-DOMINIQUE 1979; POLLOCK 1986; PEREIRA et al. 1988; MACEDONIA u. STANGER 1994; ODA u. MASATAKA 1996; POWZYK 1997; WRIGHT 1998; MARETTI et al. 2010; PATEL 2010). However, alarm calls were not recorded during my study. PETTER u. CHARLES-DOMINIQUE (1979) interpret the loud calls “ava-hee” as an alarm call. From my findings, we could not confirm this proposed function because I never encountered predators during my observation. It thus remains unknown whether the calls that we have recorded, also function as alarm calls or if woolly lemurs possess another type of alarm call. Nevertheless, these findings still confirmed that acoustic signals in western woolly lemurs are due to ancestral traits.
The vocal repertoires of *Propithecus* and *Indri* are more varied than those of *Avahi*. They still have several calls which are lacking in our recordings of western woolly lemurs. For example, *Propithecus* produces a high amplitude, tonal, and extremely frequency modulated vocalization after an individual receives aggression (Patel 2010). *Indris* give a short or a long harsh tonal vocalization during agonistic interactions. This means that primates vary enormously in the complexity of their vocal signals. One explanation of variation in vocal communication in the three genera of Indriidae might be the variation in the social structure and group size. The complexity of the social groups influences the vocal complexity used by members of the group (e.g. BLUMSTEIN u. ARMITAGE 1997; MCCOMB u. SEMPLE 2005; FREEBERG 2006). For example, ground-dwelling sciurid species with socially complex groups (i.e. many age/sex classes) produce more acoustically distinct alarm calls than species with fewer age/sex classes (BLUMSTEIN u. ARMITAGE 1997). Factors other than social complexity may contribute to the evolution of call repertoire size such as variation in the facial or laryngeal morphology, physical and/or biological habitat acoustics, and specific needs ((BLUMSTEIN u. ARMITAGE 1997). More data will probably be useful to help address the question of the relative importance of social complexity and other causal factors in the evolution of complex communication.

**Perspectives for future research**

The existence of social animals depends upon their capacity to communicate with members of their species. Vocal interactions provide the most obvious proof that individuals are communicating. Examining the vocal coordination provides important indications of the function of various signalling strategies. Antiphonal calling is typical of tropical species living in dense foliage and forming an extended pair bond (STOKES u. WILLIAM 1968). In territorial cohesive pair-living primates, duetting is proposed to serve as a mechanism for excluding intruders from an occupied territory, for maintaining inter-group spacing, and for proceeding as a strengthening of the pair bond (HAIMOFF u. GITTINGS 1985; MITANI 1985; ROBINSON et al. 1987, GEISSMANN 1999). Therefore, the analysis of the synchronization of vocal signals in western woolly lemurs is needed by testing the hypotheses that vocal exchanges are used for cooperative territorial defence and maintaining pair-bonds.

In many prosimians, scent-marking is one form of communication in which their proposed function is a territorial demarcation, ownership of resources, mate attraction, non-combative fighting, or self-advertisement (GOSLING u. ROBERTS 2001; WOLF et al. 2002;
MILLER et al. 2003; POCHRON et al. 2005). In *Propithecus*, scent-marks may be a more frequent channel of communication. Female sifakas deposit scent marks by rubbing their anogenital regions on trunks and branches, and they often urinate in such a way that their urine pours down the trunk to which they are clinging. Males exhibit similar behaviours and in addition, lay down scent marks by rubbing trunks and branches with a gland at the base of the throat (POCHRON et al. 2005; LEWIS 2006; LEWIS u. SCHAIK 2007). Scent mark could be interpreted as a second mechanism whereby animals in neighbouring groups establish and maintain relationships. *Indris* lack scent glands on the throat, chest, head, arms, and wrist, with glandular fields in evidence around the anus region (PETTER et al. 1977; POLLOCK 1975; POWZYK 1997). They do not mark territorial boundaries via anogenital marking, but achieve territorial defence through long calling (POWZYK u. MOWRY 2006). Indris are frequently seen to mark identical parts of repeatedly used arboreal routes whose functions imply identification rather than definition of an occupied area. Woolly lemurs are known to develop prominent scent glands under the chin (WARREN u. CROMPTON 1997), the function of which is unknown. Further research should study the olfactory communication in woolly lemurs. No research has yet been published on their scent-marking behaviour.

Western woolly lemurs have been observed to sleep together, groom each other, defend their territory against other groups, maintain proximity, and coordinate activities. Woolly lemurs use acoustic signalling as a major mechanism for social communication. Western woolly lemur calls serve at least two important social functions: to bring partners together and enhance cooperation and to keep competitors apart and reduce conflict. Future studies should examine to which extent information conveyed in vocalizations can be recognized and are relevant for the survival of woolly lemurs.

All in all, this thesis provided new empirical and quantified information on the biology of a previously scarcely unknown and endangered nocturnal Malagasy lemur, the western woolly lemur. Based on these findings, further empirical studies can be planned: (1) explore the different communication channels in more detail, (2) study the variation of eco-ethology and communication of this endangered lemur group across Madagascar and its relevance for taxonomy, phylogeny and dispersion, (3) provide information necessary to improve programmes for lemur monitoring, management and conservation.
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I herewith that I autonomously carried out the PhD-thesis entitled “Sociality and communication in woolly lemurs”.

No third party assistance has been used.

I did not receive any assistance in return for payment by consulting agencies or any other person. No one received any kind of payment for direct or indirect assistance in correlation to the content of the submitted thesis.

I conducted the project at the following institution: Institute for Zoology, University of Veterinary Medicine of Hannover.

The thesis has not been submitted elsewhere for an exam, as thesis or for evaluation in a similar context.

I hereby affirm the above statements to be complete and true to the best of my knowledge.
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