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3 **The role of acoustic signaling for spacing and group coordination in a nocturnal, pair-**  
4 **living primate, the western woolly lemur (*Avahi occidentalis*)**  
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3 **ABSTRACT**  
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5 **Objectives**  
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7 How social groups govern their distribution in time and space is a central question in  
8 socioecology. The aim of this study is to explore the role of acoustic signaling for spacing and  
9 cohesiveness in a nocturnal, cohesive, pair-living strepsirrhine.  
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14 **Material and Methods**  
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16 The study was conducted in northwestern Madagascar. Six pairs of *Avahi occidentalis* were  
17 radio-collared and home range usage, vocalizations and call-associated behavior recorded  
18 using GPS-based focal animal sampling. Home range size was analyzed using ArcView GIS  
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23 3.3. Calls were characterized by a multiparametric sound analysis.  
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25 **Results**  
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27 Three frequently used, acoustically distinct call types were identified: the avahee call, the  
28 whistle call, and the growling call, the latter is a soft; the two others are loud calls. Call types  
29 are given by both sexes and convey individually-specific signatures. Call types are used  
30 primarily in the locomotion context in the non-core-area of home ranges. The least common  
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avahee call is responded by the avahee call from farther away. The more common whistle  
call, given when partners become visually isolated, and the growling call emitted at close  
distances, were answered by the whistle and the growling call. Results suggest a spacing  
function for the avahee call and group coordination functions for the other call types.

55 **Discussion**  
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Our study provides first empirical evidence for a nocturnal, cohesive pair-living strepsirrhine  
that vocal signaling represents an important mechanism for spacing, group coordination and  
decision making. Findings contribute to a better understanding of the evolutionary roots of  
primate vocal communication.

## INTRODUCTION

A major question in socio-ecology is how pairs coordinate group movement and maintain group cohesiveness (Boinski and Garber, 2000; Couzin and Krause, 2003; de Waal et al., 2003; King and Sueur, 2011). Haplorrhine primates (except the orangutan) and diurnal Malagasy lemurs live in permanent social groups in which group members cooperate in foraging, predator detection and defense, offspring rearing or resource defense by using elaborate sets of visual, tactile, olfactory and auditory signals for social communication (Cheney and Seyfarth, 1990; Zimmermann, 1992; Hauser, 1996; Clarke et al., 2006; Röper et al., 2014). In the auditory domain, loud calls (Marten and Marler, 1977; Waser and Waser, 1977; Waser and Brown, 1984), choruses (Hall and DeVore, 1965; Tenaza, 1976; Geissmann and Mutschler, 2006), songs and duets (Pollock, 1986; Cowlshaw, 1992; Geissmann and Mutschler, 2006) are often used for inter-group spacing and group reunion, whereas soft vocalizations are given to regulate group coordination and intra-group cohesion (e.g. African elephant: Poole et al., 1988; Golden brown mouse lemur: Braune et al., 2005; redfronted lemur: Pflüger & Fichtel, 2012; Black howler monkey: da Cunha and Byrne, 2006; Spider monkey: Ramos-Fernández, 2005; Spehar and Di Fiore, 2013; gibbon: Clarke et al., 2015).

Malagasy lemurs represent a monophyletic group including nocturnal, cathemeral and diurnal species living in highly diverse social systems (e.g. Müller and Thalmann, 2000), making them an ideal model group for understanding the impact of phylogeny, social complexity and activity on the evolution of acoustic mechanisms regulating inter-group spacing and group coordination in primates (Braune et al., 2005). To date, data on the role of vocal communication for inter-group spacing and intra-group coordination are available for diurnal group- and pair-living as well as for nocturnal, solitary-foraging lemur species living in dispersed social systems or in pairs. Thus, diurnal Indriidae, such as the pair-living indris or group-living sifakas are known to use contagious calling, loud duetting or chorusing for

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3 territory demarcation and loud alarm calls (roars) for advertising the detection of disturbances  
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5 or predators (Maretti et al., 2010; Fichtel and Kappeler, 2011). Soft vocalizations (e.g. hums  
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7 in indris; grumbles calls in sifakas) are described regulating contact with other group  
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9 members at short distances (Pollock, 1975; Petter and Charles-Dominique, 1979; Macedonia  
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11 and Stanger, 1994; Maretti et al., 2010; Patel and Owren, 2012). Nocturnal lemurs which  
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13 form permanent sleeping groups, but forage solitarily during the night, such as mouse lemurs,  
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15 use acoustic signals in the context of mating, intra-group cohesion (mother- infant, sleeping  
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17 group reunions) and group coordination (Hafen et al., 1998; Braune et al., 2005; Scheumann  
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19 and Zimmermann, 2007b), as well as during conflicts with con- and heterospecifics  
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21 (Zimmermann, 2010; Zimmermann, 2013; Zimmermann et al., 2013). Olfactory mechanisms  
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23 seem to be important for regulating the distribution of groups in space (Braune et al., 2005)  
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25 and avoiding predators (Sündermann et al., 2008; Kappel et al., 2011). For nocturnal lemurs  
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27 with a dispersed pair system, such as sportive lemurs, a broad variety of different loud call  
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29 types are described, which are arranged in complex series to regulate space use and  
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31 cohesiveness between pair partners and neighbors (e.g. Rasoloharijaona et al., 2006; Méndez-  
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33 Cárdenas and Zimmermann, 2009; Rasoloharijaona et al., 2010).

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38 Until now, empirically based bioacoustic studies of nocturnal cohesive pair-living primates  
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40 have been lacking. To collect first empirical data and embed them into the evolution of  
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42 mechanisms governing primate group coordination in time and space, we studied the western  
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44 woolly lemur (*Avahi occidentalis*), distributed in the dry deciduous forests of northwestern  
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46 Madagascar. These weasel-sized lemurs that weigh approximately 1 kg (Ramanankirahina et  
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48 al., 2011), form permanent pairs in which pair partners forage together during the night and  
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50 sleep together at safe sleeping sites in trees with dense foliage during the day (Albignac,  
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52 1981; Warren and Crompton, 1997; Ramanankirahina et al., 2012). As do sportive lemurs,  
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54 woolly lemurs belong to the so-called clingers and leapers (Warren, 1997; Warren and  
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56 Crompton, 1997), and are able to move rapidly through dense forests. In contrast to sportive  
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3 lemurs, woolly lemurs are folivorous specialists, selecting underrepresented food resources  
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5 for which pairs seem to compete (Thalmann, 2001). The sexes are monomorphic and do not  
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7 differ in body mass and size (Ramanankirahina et al., 2011). Pair partners interact extremely  
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9 peacefully, although females are dominant in the feeding context (Ramanankirahina et al.,  
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11 2011). The mean home range size of pairs was estimated to be about 1.59 ha (Warren and  
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13 Crompton, 1997). Woolly lemurs are the only nocturnal representative of the family Indriidae.  
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15 Information on their vocalizations is limited so far. Petter and Charles-Dominique (1979)  
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17 were the first and only authors displaying spectrographic representations of the calls.  
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19 However, they did not provide empirical information on the callers and call usage, nor on the  
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21 geographical origin of the callers (Table 1). Harcourt (1991), Warren and Crompton (1997),  
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23 and Thalmann (2003), studying feeding ecology, locomotion energetics and social behavior of  
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25 woolly lemurs described some frequently heard calls as avahee call, whistle call and growling  
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27 call, and speculated on their function (Table 1), but neither presented empirical data on their  
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29 acoustic structure nor on their usage.  
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Table 1

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Thus, our study aims i. to acoustically characterize these qualitatively described call types in woolly lemurs, and ii. To explore for the first time their suggested functions. For the latter analysis we linked the structure of the acoustically characterized call types to the sound-associated context. Furthermore, by performing a multivariate acoustic analysis, we tested for individuality in call structure. Likewise, by relating caller positions for the respective call types to the home range of the respective pair, we explored the spatial distribution of calling positions.

## **MATERIALS AND METHODS**

### **Study area and animals**

The study was carried out in the research area JBA (Jardin Botanique A, 30.6 ha; 16°19'S, 46°48'E) 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 studied. For one pair the female changed during the observation period.

### **Data collection**

Each animal was darted, weighed and morphometrically characterized and fitted with a radiotransmitter on a backpack (for more details on darting focal animals, radiotelemetric methods, group sizes and focal animal contact times, see Ramanankirahina et al., 2011; Ramanankirahina et al., 2012). The median body length was 20 cm for males and females, the mean body mass was 825 g for males and 999g for females with no significant difference between sexes (see Ramanankirahina et al., 2011). GPS-based radio telemetry was used to monitor behavioral activity and habitat usage of focal animals. Using a portable receiver and an antenna, a radio-collared individual was followed between May to November 2008. Each focal animal was 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.). Unfortunately, not more than one focal animal could be observed in one night because of budget limitations. The total contact time was 667 hours (Ramanankirahina et al., 2011). One female could only be followed for October and November for a total of 19 hours contact time since she had been caught first in October. For the pair where the female changed during observation, the first female was observed during May and June and the second female from August to November. Since both females were associated with the same male, data of both females were treated as

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3 one female pair partner for further analyses, as done in two previous papers  
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5 (Ramanankirahina et al., 2011; Ramanankirahina et al., 2012).  
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7 Focal animal sampling with continuous recording was conducted (Altmann, 1974;  
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9 Martin and Bateson, 1993). The movement pattern of a focal animal was noted by taking the  
10 geographical positions every 10min (GPSMAP 60CSx, Garmin, mean error < 10 m). Calls  
11 were classified into three major call types: avahee call, whistle call and growling call. We  
12 collected information regarding the identity of the caller, the time, the type of the tree where  
13 the focal individual vocalized (resource site=site used for feeding or sleeping, or non-resource  
14 site=all other sites, except feeding and sleeping sites). Calling context (events inducing a call)  
15 was recorded, as well as the focal animal's activity, e.g. resting, feeding or locomotion,  
16 according to Méndez-Cárdenas and Zimmermann (2009). If a call was responded by another  
17 individual (meaning immediately after the focal animal gave its call), the call type of the  
18 response call was recorded. If the focal animal gave a call immediately after we had heard  
19 another animal calling, the call type of its response was recorded as a response call to another  
20 individual's call.  
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### 38 **Determination of home range size and overlapping area**

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40 GPS coordinates per half night were entered immediately after a focal animal night  
41 into ArcView GIS 3.3 (ESRI). Home range size was assessed according to common methods  
42 (Ganas and Robbins, 2005; Harris, 2006) and corrected for obvious outliers: The size was  
43 determined by using GPS positions (Male: median, 532 points/individual, range 427-661  
44 points, N=6; Female: median, 503 points/individual, range 186-645 points, N=6) collected  
45 every 10min during the nocturnal focal animal sampling. To be comparable with most other  
46 lemur studies, we estimated home range sizes and overlaps between partners and pairs by  
47 using the 100% Minimum Convex Polygon (MCP). To determine if there was a sex  
48 difference in home range size, the home range sizes of males and females were compared  
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3 using the Mann-Whitney U test. Additionally, the proportions of home range overlaps  
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5 between the different focal individuals were calculated by an overlay procedure of the  
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7 geoprocessing extension in ArcView 3.3. Mann-Whitney U tests were used to examine  
8  
9 whether the proportion of overlap between home ranges of same sex neighbors (male/male,  
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11 female/female), opposite sex neighbors (male/female) or pair partners differed.  
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### 13 14 15 16 **Acoustic recording and analyses**

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18 Vocalizations were recorded using a Sennheiser directional microphone (ME67,  
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20 Sennheiser, Wedemark, Germany: frequency range: 40 – 20 000 Hz) with a windshield,  
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22 linked to a stereo cassette recorder (Sony Professional WM-D6C; Sony, Japan) onto audio  
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24 recording cassettes (Sony super chrome class UX-S IECII/Type II). All vocalizations were  
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26 digitized with a sample frequency of 44.1 kHz and a sample size of 16 bit using Batsound Pro  
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28 3.31 (Petterson Elektronik AB, Uppsala Sweden) and stored as wav?? files.  
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32 In total, 733 vocalizations were visually inspected using spectrograms of the software  
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34 Batsound Pro 3.31 (FFT: 512, Hanning window) and visually classified into three call types:  
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36 (1) the avahee call, (2) the whistle call, and (3) the growling call (Figure 1). Based on this  
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38 sample, 405 calls of high quality (i.e. calls not disturbed by background noise and minimum  
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40 amplitude difference of 7% between background noise and maximum amplitude of the call)  
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42 were selected to conduct a multi-parametric sound analysis using call-type specific self-  
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44 written macros for the software Signal 4.1 (Kim Beeman, Engineering design). The avahee  
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46 call consists of two harmonic syllables (Figure 1), for which four temporal and nine spectral  
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48 parameters were measured (Table 2). The first syllable is characterized by a clear fundamental  
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50 frequency, often not visible in the second syllable. Thus, in the latter we characterized the  
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52 dominant frequency band and the most prominent side-band. We measured for the first  
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54 syllable acoustic parameters related to the fundamental frequency (F0) and for the second  
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56 syllable acoustic parameters related to the dominant frequency (Fd) band and the first side  
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3 band above or below the dominant frequency. The whistle call is harmonic and characterized  
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5 by an almost constant narrow frequency band (Figure 1). For the whistle calls one temporal  
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7 and four spectral parameters were measured (Table 2). The growling call consists of a high  
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9 number of broadband pulses (Figure 1). Measurements of pulse duration and distance  
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11 between pulses were related to the first five pulses of a call. For the growling call, 11  
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13 temporal and one spectral parameter were measured (Table 2).  
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23 Figure 1  
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36 For further statistical analysis only individuals that contributed at least five calls were  
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38 considered. To characterize the acoustic structure of the calls, we calculated the mean and  
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40 standard deviation of each parameter per call type based on the individual means. To  
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42 investigate individual differences in Avahi vocalizations, we conducted analyses for each call  
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44 type as follows: first, to investigate whether acoustic parameters differ statistically between  
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46 individuals, we performed a One-way ANOVA and calculated the effect size using  $\eta^2$ . To  
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48 control for multiple testing we applied the Fishers Omnibus test combining multiple p-values  
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50 (Haccou and Melis, 1994). Second, to investigate whether calls can correctly be classified to  
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52 the respective individual, we performed an independent DFA and a nested permuted  
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54 discriminant function analysis (pDFA; Mundry and Sommer, 2007). To rule out that acoustic  
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56 parameters used for both DFAs did not correlate with each other, prior to the DFA we  
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3 performed a correlation analysis using a Pearson correlation. We selected acoustic parameters  
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5 with a correlation coefficient  $< 0.500$ . For the independent DFA, we calculated the degree of  
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7 agreement between predicted and observed classification using the Kappa test (Scheumann et  
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9 al., 2007c). According to the literature (Landis and Koch, 1977, Stemler, 2001) the level of  
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11 agreement is defined as follows: Cohen's kappa  $< 0.00$  poor agreement, 0.00–0.20 slight  
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13 agreement, 0.21-0.40 fair agreement, 0.41-0.60 moderate agreement, 0.61-0.80 substantial  
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15 agreement and 0.81-1.00 almost perfect agreement. For the pDFA we used subject as test  
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17 factor and sex as control factor. The number of permutation was set at 1000 and the number  
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19 of random selections was set at 100.  
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#### 25 **Analysis of calling activity, location, context and counter-calling**

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27 For analysing the calling activity, we calculated the call rate of the respective call type  
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29 for each individual by dividing the number of calls of the respective call type by the total  
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31 contact time per hour per individual. Due to the fact that data were not normally distributed,  
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33 non-parametric statistics were performed. To investigate sex differences in the calling  
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35 activity, we compared the call rate of the respective call types between sexes using Mann-  
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37 Whitney U tests.  
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40 To investigate the effect of resource site, we compared the call rate between the  
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42 resource and the non-resource site. Since the duration an individual spent at the resource or  
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44 non-resource site was not equally distributed (82% of the time individuals spent at the  
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46 resource site and 18% at the non-resource site), we first calculated the call rate per minute per  
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48 individual at the resource site. Thus, we counted the number of calls and divided them by the  
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50 duration in minutes the individual was observed at the respective location. Then, we  
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52 compared the call rate between resource and non-resource site using the Wilcoxon signed-  
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54 rank test.  
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3 To investigate the effect of context, we compared the call rate between the three main  
4 contexts which were observed shortly before the focal individual vocalized: locomotion,  
5 resting and feeding. Since the duration an individual spent in the respective contexts varied  
6 strongly between contexts (% of total contact time a context was observed: locomotion: 1%,  
7 resting: 58%; feeding: 37%), we first calculated the call rate per minute per context. Thus, we  
8 counted the number of calls and divided them by the time the individual was observed in the  
9 respective context per minute. Then, we compared the call rate between the three contexts  
10 using the Friedman test. When the Friedman test was significant, pairwise comparisons were  
11 conducted using the Wilcoxon signed-rank test. To control for multiple testing the Bonferroni  
12 correction was used ( $p_{\text{corr}} = \text{No. of comparisons} * p\text{-value}$ ).  
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25 To analyze counter-calling, we analyzed, at first, for each call type separately whether  
26 the calls of the focal animal were given spontaneously or as response to calls. Calls were  
27 counted as response call when they occurred immediately after a call of another individual.  
28 Thus, we calculated for each focal animal and call type the percentage of spontaneous calls  
29 and calls in response to avahee, whistle or growling calls from other individuals. To  
30 investigate whether other individuals responded to the call types of the focal animals, we  
31 calculated for each focal animal and call type the percentage of calls which elicited no  
32 response, avahee, whistle or growling calls.  
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### 45 **Spatial distribution of the calling positions**

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47 The calling position for the three call types of each pair was overlaid with the home  
48 range by using ArcView GIS 3.3 to explore if calls were emitted at the core or non-core area  
49 of the home ranges. To define the non-core and core area of the home ranges, the 95% (non-  
50 core) and 50% (core) Fixed Kernel method was used (Horner and Powell, 1990; Harris,  
51 2006).  
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3 The recorded geographical position of the pair's calling position (place where a focal  
4 individual of the respective pair emitted a call) was mapped on the Kernel home range area.  
5 From the geoprocessing extension in ArcView 3.3 we quantified the number of caller  
6 positions for each pair within the core (Kernel 50%) and the non-core area (Kernel 95%). To  
7 investigate whether significant more calling positions were observed within the core  
8 compared to the non-core area, we calculated an observed versus expected Chi square test  
9 based on the number of calling positions in the respective areas. Since the 50% Kernel  
10 contour represents the 50% probability that the pair was found in the core area (Horner and  
11 Powell, 1990), the expected frequency for an equal distribution was set at 50% for the core  
12 area.  
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### 27 **Ethical considerations**

28 All procedures adhered to the legal requirements of Madagascar, and were approved by the  
29 Ministere de l'Environnement et des Forêts and Madagascar National Parks. This research  
30 was conducted in accordance with the American Society of Primatologists and German  
31 Society of Primatologists (GfP) ethical principles for the treatment of primates.  
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## 40 **RESULTS**

### 41 **Home range size and overlapping areas**

42 Using the MCP method, the median home range size of pairs was 1.96 ha (min-max:  
43 1.2-3.1 ha). Home ranges of pairs overlapped about 25% (Median, min-max: 10%-51%) with  
44 those of neighboring pairs. One pair showed no overlapping area with the other focal pairs  
45 (Figure 2).  
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56 For males, median home range size was 1.79 ha (min-max: 1.08-2.72 ha), for females  
57 1.57 ha (min-max: 1.1-3.01 ha). Home range size did not differ significantly between sexes  
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3 (Mann-Whitney  $U=15$ ,  $N_m=6$ ,  $N_f=6$ ,  $p=0.631$ , Figure 2). The home ranges of pair partners  
4 overlapped strongly with each other. Thus, home range of males overlapped with the  
5 respective female pair partner about 85% (Median, min-max: 65%-97%) of their total home  
6 range and home range of females overlapped with the respective male pair partner about 93%  
7 (Median, min-max: range 88%-100%, Figure 2). There was no significant difference in the  
8 percentage of home range overlap between pair partners (Mann-Whitney  $U=8$ ,  $N_m=6$ ,  $N_f=6$ ,  
9  $p=0.109$ ). In contrast to the strong overlap between the home range of pair partners,  
10 neighboring animals showed a low percentage of home range overlap for both sexes. Home  
11 range of males overlapped with neighboring males about 13% (Median, min-max: 7%-44%)  
12 of their total home range, whereas home range of females overlapped with neighboring  
13 females about 6% (Median, min-max: 3%-12%). Thus, the overlap between male home  
14 ranges was significantly larger than between female home ranges (Mann-Whitney  $U=2$ ,  $N_m=5$   
15  $N_f=5$ ,  $p=0.028$ ). Home ranges of males overlapped with neighboring females about 12%  
16 (Median, min-max: 6%-20%) of their total home range and home ranges of females  
17 overlapped with neighboring males about 9% (Median, min-max: range 8%-38%).  
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38 Figure 2  
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#### 47 **Acoustic characteristics of call types**

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49 The avaahee call ( $N=6$ ,  $n=113$ ; Figure 1, Table 3) represents a loud, harmonic call  
50 consisting of two syllables. The first syllable showed a fundamental frequency with several  
51 harmonics, whereas the second syllable showed a dominant frequency band with side bands,  
52 the fundamental frequency not being visible in the spectrogram. The mean duration of the first  
53 syllable was  $107 \pm 9$  ms and for the second syllable  $255 \pm 53$  ms, respectively. The total  
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3 duration of the whole avaahee call was  $393 \pm 57$  ms. The first syllable was characterized by a  
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5 harmonic structure with a fundamental frequency of  $707 \pm 84$  Hz. The second syllable was  
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7 characterized by a dominant frequency of  $4118 \pm 348$  Hz. Side-bands could be observed  
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9 around this dominant frequency. The mean frequency distance between the dominant  
10  
11 frequency and the first side band above or below was  $937 \pm 89$  Hz.  
12

13  
14 The whistle call (N=11, n=195; Figure 1, Table 3) is a loud call of almost constant  
15  
16 frequency. It was given as a single call or in a call series. The mean call duration was  $1268 \pm$   
17  
18  $304$  ms and the peak frequency was  $4353 \pm 220$  Hz, respectively.  
19

20  
21 The growling call (N=7, n=97; Figure 1, Table 3) is a soft and broadband call  
22  
23 consisting of rapidly repeated short broadband pulses. The call duration was  $941 \pm 228$  ms  
24  
25 and a call contained  $17 \pm 4$  pulses of almost constant duration  $23-26$  ms  $\pm 2-3$ . The peak  
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27 frequency was about  $4538 \pm 1020$  Hz.  
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Table 3

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### Acoustic discrimination of individuals

For the avaahee call all acoustic parameters differed significantly between individuals ( $F \geq 2.73$ ,  $df=5$ ,  $N=113$ ,  $p \leq 0.023$ ;  $0.113 \leq \eta^2 \leq 0.419$ ; Fisher Omnibus test:  $\chi^2=300.47$ ,  $df=26$ ,  $p < 0.001$ ; Table 3). Based on the correlation analysis, six parameters were selected to calculate the DFAs: duration of the first syllable (Dur1), gap of two successive calls (Gap), total duration of the call (Dur), fundamental frequency of the first syllable (F0), maximum dominant frequency (Fdmax) and difference between dominant frequency and sideband (DiffFd-s). An independent DFA correctly assigned 70.8 % of the calls to the correct individual (cross-validation: 66.4%), with moderate agreement of classification ( $k=0.544$ ,

1  
2  
3 p<0.001). Results of the pDFA controlling for sex support that calls were classified  
4  
5 significantly correctly to the respective individual (selected cases: 75.27% correctly classified,  
6  
7 chance level=47.81%, p=0.001; cross-validation: 57.48% correctly classified, chance  
8  
9 level=21.67%, p= 0.001, Table 4).

10  
11 For the whistle call, all acoustic parameters differed significantly between individuals  
12  
13 ( $F \geq 2.89$ ,  $df=10$ ,  $N=195$ ,  $p \leq 0.002$ ;  $0.136 \leq \eta^2 \leq 0.269$ ; Fisher Omnibus test:  $\chi^2=146.81$ ,  $df=10$ ,  
14  
15  $p < 0.001$ ; Table 3). Based on the correlation analysis, three parameters were selected to  
16  
17 calculate the DFAs: total duration of the call (Dur), minimum fundamental frequency (Fpmin)  
18  
19 and bandwidth (Fpbandwith). An independent DFA correctly assigned 31.3 % of the calls to  
20  
21 the correct individual (cross-validation: 24.6%), with fair agreement of classification  
22  
23 ( $k=0.211$ ,  $p < 0.001$ ). The results of the pDFA controlling for sex revealed that calls were  
24  
25 classified significantly correctly to the respective individual (selected cases: 33.10% correctly  
26  
27 classified, chance level=19.45%,  $p=0.001$ ; cross-validation: 16.48% correctly classified,  
28  
29 chance level=8.86%,  $p=0.011$ , Table 4).

30  
31 For the growling calls almost all acoustic parameters differed significantly between  
32  
33 individuals ( $F \geq 2.31$ ,  $df=6$ ,  $N=97$ ,  $p \leq 0.040$ ,  $0.134 \leq \eta^2 \leq 0.383$  except for the duration of pulse 1  
34  
35 and 5  $F \leq 2.18$ ,  $df=6$ ,  $N=97$ ,  $p \geq 0.053$ ,  $\eta^2 \leq 0.127$ ; Fisher Omnibus test:  $\chi^2=154.56$ ,  $df=24$ ,  
36  
37  $p < 0.001$ ; Table 3). Based on the correlation analysis six parameters were selected to calculate  
38  
39 the DFA: total duration of the call (Dur), peak frequency (Peak) and duration of the second  
40  
41 and fourth pulse (DurPulse2 and DurPulse4) and distance between first and second  
42  
43 (DisPulse1-2) and between third and fourth pulse (DisPulse3-4). An independent DFA  
44  
45 correctly assigned 56.7 % of the calls to the correct individual (cross-validation: 50.5%), with  
46  
47 moderate agreement of classification ( $k=0.420$ ,  $p < 0.001$ ). The results of the pDFA controlling  
48  
49 for sex revealed that calls were classified significantly correctly to the respective individual  
50  
51 (selected cases: 65.86% correctly classified, chance level=50.52%,  $p=0.015$ ; cross-validated  
52  
53 cases: 29.15% correctly classified, chance level=17.55%,  $p=0.024$ , Table 4).

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Table 4

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### **Calling activity and call types**

The highest calling rate could be observed for growling calls with a median of 0.833 calls/h, followed by whistle calls with a median of 0.406 calls/h. The lowest calling rate was observed for avahee calls with a median of 0.070 calls/h. The avahee call was produced with the median rate of 0.071/h (25%-75% quartile: 0.020-0.140/h) by males and 0.087/h (25%-75% quartile: 0.038-0.385/h) by females. The median rate of the whistle call was 0.516/h (25%-75% quartile: 0.325-0.568/h) by males and 0.318/h (25%-75% quartile: 0.124-0.434/h) by females. The growling call was emitted with the median rate of 0.794/h (25% -75% quartile: 0.514-2.014/h) by males and 0.922/h (25%-75% quartile: 0.470-3.324/h) by females. Sexes showed no significant difference in calling rate for each call type (avahee:  $U=14$ ,  $N_m=6$ ,  $N_f=6$ ,  $p=0.522$ ; whistle:  $U=7$ ,  $N_m=6$ ,  $N_f=6$ ,  $p=0.078$ ; growling:  $U=15$ ,  $N_m=6$ ,  $N_f=6$ ,  $p=0.631$ ).

### **Calling rate, location, call associated context and antiphonal-calling**

The calling rate of the three call types was significantly higher at the non-resource than the resource site ( $T=1$ ,  $N=12$ ,  $p\leq 0.004$ ,  $p_{\text{corr}}\leq 0.012$  for all call types) and differed significantly between contexts ( $\chi^2\geq 9.556$ ,  $N=12$ ,  $df=2$ ,  $p\leq 0.008$ ,  $p_{\text{corr}}\leq 0.024$  for all call types, Figure 3).

For all three call types the calling rate during locomotion was significantly higher than during resting and feeding ( $T\leq 1.50$ ,  $N=12$ ,  $p\leq 0.013$ ,  $p_{\text{corr}}\leq 0.039$  for all call types; Figure 3), whereas no significant difference between the feeding and the resting contexts could be found



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3 for the avahee and growling call ( $T \geq 3.50$ ,  $N=12$ ,  $p \geq 0.107$ ) nor after applying the Bonferroni  
4  
5 correction for the whistle call ( $T=5.75$ ,  $N=12$ ,  $p \geq 0.030$ ,  $p_{\text{corr}}=0.09$ ).  
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18 A total of 89 avahee calls were recorded from 11 focal animals, both when pair  
19 partners were both visible to observer and when one partner was out of sight. 68 of 89 avahee  
20 calls (76.40%) were spontaneously given and 17 avahee calls (19.1%) were given in response  
21 to an avahee call from another individual. 79 of the 89 avahee calls (88.76%) of the focal  
22 animals evoked no vocal response. In 8 cases another individual answered an avahee call. In  
23 the majority of cases where the focal animal responded to an avahee call or other individuals  
24 responded to an avahee call of the focal animal, an avahee call was recorded as response call.  
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34 For the whistle call, 271 calls from all 12 focal animals could be recorded when pair  
35 partners travel without visual contact to each other (one pair partner out of sight of observer).  
36 254 whistle calls (93.73%) were produced spontaneously. 14 whistle calls (5.17%) were given  
37 in response to a whistle call from another individual. 248 of the 271 whistle calls (91.51%) of  
38 the focal animals evoked no vocal response. Interestingly, in 12 cases (4.43%) another  
39 individual answered by producing a growling call and in 9 cases by also producing a whistle  
40 call (3.32%). Thus, in the majority of cases where the focal animal responded to a whistle call  
41 or other individuals responded to a whistle call of the focal animal, the growling call was  
42 recorded in response to a whistle call.  
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54 A total of 855 growling calls were recorded from all focal individuals, when pair  
55 partners were close to each other (pair partners could be seen by observer). The majority of  
56 growling calls (769, 89.94%) were given spontaneously, but 69 (8.07%) were produced in  
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3 response to a whistle call of another individual. 850 of the 855 whistle calls (99.42%) of the  
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5 focal animals evoked no vocal response. To sum up, in the majority of cases focal animals  
6  
7 responded to whistle calls using a growling call, whereas growling calls themselves evoked  
8  
9 less vocal responses.  
10

### 11 12 13 14 **Spatial distribution of calling positions** 15

16 Using the 95% Kernel, the median home range size of pairs was 1.61 ha (min-max: 1.1  
17  
18 – 2.94 ha; Figure 4–6) which is comparable to the MCP method. The median core area of  
19  
20 pairs was 0.14 ha (min-max: 0.06 – 0.38 ha) using the 50% Kernel. No overlapping of the  
21  
22 core area existed between neighboring pairs or neighboring individuals. Plotting the caller's  
23  
24 positions per pair in the respective pair home range, 87% of avahee (Median, 25-75%  
25  
26 quartile: 50-100%, Figure 4), 86% of whistle (Median, 25-75% quartile: 60-97%, Figure 5)  
27  
28 and 84% of growling call positions (Median, 25-75% quartile: 73-94%, Figure 6) occurred  
29  
30 outside the core area of the respective pairs. These findings were statistically supported: for  
31  
32 each call type, significantly more calling positions than expected by chance were found  
33  
34 outside of the core area (avahee:  $\chi^2=26.98$ ,  $df=1$ ,  $N=99$ ,  $p<0.001$ ; whistle:  $\chi^2=84.14$ ,  $df=1$ ,  
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36  $N=271$ ,  $p<0.001$ ; growling:  $\chi^2=342.32$ ,  $df=1$ ,  $N=855$ ,  $p<0.001$ ).  
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Figure 4

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Figure 5

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Figure 6

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5 **DISCUSSION**  
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7 Our study suggests for the first time that in a nocturnal, cohesive pair-living primate,  
8 the woolly lemur, acoustic signaling acts as an important mechanism to govern pair  
9 coordination and inter-group spacing. Call structure and usage of the reported three call types  
10 provided the first empirical evidence for their functions. Findings will be discussed regarding  
11 the suggested functions reported in the literature. Furthermore, we will compare findings with  
12 other lemur species to explore two commonly discussed hypotheses for the evolution of  
13 communicative complexity in primates, the phylogenetic and the social complexity  
14 hypothesis.  
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30 **Vocalizations of woolly lemurs and their potential functions**  
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32 In our study we investigated the three most common vocalizations of the western  
33 woolly lemur, the avahee call, the whistle call and the growling call, with regard to their  
34 acoustic structure and usage to deduce their function. All three call types were used primarily  
35 in the locomotion context in the non-core-area of home ranges. Additionally, specific  
36 differences between call types were observed in relation to loudness, calling rate and  
37 antiphonal calling behavior suggesting specific functions for spacing and social cohesion. The  
38 least common avahee call was mainly responded by the avahee call. The more common  
39 whistle call, given when partners become visually isolated, and the growling call, emitted at  
40 close distances, was answered by the whistle or the growling call. Avahee and growling calls  
41 displayed statistically moderate individual discrimination, while discrimination in the whistle  
42 call was only fair.  
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56 As outlined in the following, our findings support some speculations (Table 1) in the  
57 literature on the function of these call types for intra- and inter-group coordination  
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3 empirically. The avahee call was given with high amplitude and displayed energy  
4  
5 concentrated at lower frequencies. These acoustic characteristics are known to minimize  
6  
7 degradation and attenuation by high ambient noise and maximize sound transmission and  
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9 localization over longer distances (Marten and Marler, 1977; Waser and Waser, 1977; Waser  
10  
11 and Brown, 1984). Thus, this call type can be considered a loud call. The avahee call rarely  
12  
13 occurred compared to the second loud call type, the whistle. Both call types were given in the  
14  
15 same context, namely locomotion in the non-core area. In contrast to the whistle call, the  
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17 avahee call was answered by the avahee call from individuals, which seemed to be farther  
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19 away and thus most probably not pair partners. Direct agonistic conflicts between neighboring  
20  
21 pairs were never observed in the study period. These findings support that the avahee call is  
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23 used for territory demarcation as suggested by Warren and Crompton (1997) and has an inter-  
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25 group spacing function.  
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30 In contrast to the avahee call, the whistle call and the growling call were given with  
31  
32 much higher rates. Whistle calls were responded by growling calls, suggesting that both call  
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34 types function for the coordination of pair movement and thus contribute to pair cohesion and  
35  
36 decision making. Both call types differ in sound amplitude. The growling call has fairly low  
37  
38 amplitude with call attributes that are recognizable only at short distances and that also  
39  
40 evoked less vocal responses than the two other call types. In the majority of cases, both pair  
41  
42 partners were together when producing growling calls, suggesting that the growling call is  
43  
44 given as a close-distance location marker to keep in contact as is also described for diurnal  
45  
46 lemurs (e.g. sifakas: Trillmich et al., 2004; for redfronted lemurs: Pflüger and Fichtel, 2012).  
47  
48 In contrast, the whistle call can be considered as a loud call due to its high amplitude and the  
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50 fact that it is emitted at farther distance when visual contact between pair partners is broken  
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52 by vegetation, comparable to diurnal lemurs living in cohesive social systems, e.g. the lost  
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54 call in sifakas (Trillmich et al., 2004) or the meows in ringtailed lemurs (Oda, 1996) and  
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56 redfronted lemurs (Pflüger and Fichtel, 2012). Findings support that the whistle call functions  
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3 as a means of communication between pair partners travelling and foraging together at farther  
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5 distances (Warren and Crompton, 1997).  
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7         Acoustic analysis revealed individual distinctiveness across all call types, with  
8  
9 variation in agreement between observed versus predicted classification. Whereas the  
10  
11 discriminant analysis revealed a moderate agreement for the avahee and growling call,  
12  
13 characterized by a multiple set of acoustic parameters, a fair agreement was yielded for the  
14  
15 whistle call. The tonal whistle call displays a much simpler acoustic structure than the other  
16  
17 two call types, resulting in the fact that only two non-correlating parameters could be included  
18  
19 in the discriminant analysis. These lower numbers of parameters may also affect the result of  
20  
21 statistical discrimination. A further explanation for the statistically yielded low classification  
22  
23 may be sample size. We expect that correct classification may increase when more calls per  
24  
25 individual become available, enabling a better balanced data set. Furthermore, future studies  
26  
27 should pay special attention to playback experiments to explore whether the statistically  
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29 revealed differences are biologically meaningful and sufficient to identify and discriminate  
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31 pair partners and neighbors.  
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36         No sex difference in calling rate for all call types was found. This suggests that sexes  
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38 play an equal role in keeping contact and/or leading travelling movements and that males do  
39  
40 not play a more prominent role in resource defense than females, e.g. in helping females save  
41  
42 energy for other beneficial purposes such as investment in offspring (e.g. Jolly, 1984; Warren  
43  
44 and Crompton, 1997; Méndez-Cárdenas and Zimmermann, 2009) by overtaking the expenses  
45  
46 for loud calling. However, vocal displays are only one means of defending a territory,  
47  
48 olfactory demarcation is another. Western woolly lemurs exhibit chin glands (Hill, 1953) and  
49  
50 in our study chin marking was observed at resource sites. These findings coincide with  
51  
52 olfactory behavior of sifakas (Pochron et al., 2005; Lewis, 2006; Lewis and van Schaik, 2007)  
53  
54 and suggest that multimodal signaling using olfactory and acoustic signaling serves as a  
55  
56 mechanism for inter-group spacing. Thus, it would be interesting in further studies to explore  
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3 under which conditions multimodal signaling is involved in territorial advertisement and  
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5 defense.  
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### 8 9 **The effect of social complexity and phylogeny on vocal communication**

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11 The social complexity hypothesis (e.g. McComb and Semple, 2005; Freeberg et al.,  
12 2012; Pollard and Blumstein, 2012) predicts that increases in social complexity may have  
13 driven the evolution of communication. The phylogenetic hypothesis (e.g. Harvey and Pagel,  
14 1991; Ord and Garcia-Porta, 2012) argues that signal complexity between closely related  
15 members of a taxonomic group is more similar than between more distantly related taxonomic  
16 groups, based on the shared evolutionary history. Comparable bioacoustic data to our study in  
17 nocturnal woolly lemurs are available from the nocturnal sportive lemurs of the taxonomic  
18 family Lepilemuridae, which are considered as pair-living (Rasoloharijaona et al., 2003;  
19 Rasoloharijaona et al., 2006; Méndez-Cárdenas and Zimmermann, 2009) and from the diurnal  
20 indris and sifakas (Pollock, 1975; Petter and Charles-Dominique, 1979; Macedonia and  
21 Stanger, 1994; Maretti et al., 2010; Patel and Owren, 2012) of the same taxonomic family  
22 (Indriidae), the former with the same (pair-living), the latter with a more complex social  
23 system (living in cohesive groups). This comparable data set allows us to explore these two  
24 hypotheses.  
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27  
28 According to the social complexity hypothesis (see above), taxa that share a similar  
29 social system should match in vocal complexity, even if they belong to different taxonomic  
30 families within the Lemuriformes. Both, the Milne Edwards' sportive lemur and the western  
31 woolly lemur, are clingers and leapers of comparable body size. Both species share the same  
32 activity pattern and habitat and thereby the same predation risks as well as the same ambient  
33 noise and habitat transmission conditions for acoustic signaling. Both species are described as  
34 pair-living, form long-term pair bonds, but species differ in pair cohesion during foraging  
35 (Ramanankirahina et al., 2011, 2012; Rasoloharijaona et al., 2003; Rasoloharijaona et al.,  
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3 2006; Méndez-Cárdenas and Zimmermann, 2009). When we compare the vocal behavior of  
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5 the western woolly lemur (Indriidae) to the Edwards' sportive lemur (Lepilemuridae), the  
6  
7 vocal behavior is quite distinct. In the context of intra-group cohesion and inter-group spacing  
8  
9 woolly lemurs of both sexes use three different call types, two of them loud, the third soft,  
10  
11 each in a slightly different context. In contrast, sportive lemurs govern social cohesion and  
12  
13 inter-group spacing by using a large set of nine different loud call types, which are in part sex-  
14  
15 specific. Furthermore, pair partners in the latter species often engage in duetting at resource  
16  
17 sites (Rasoloharijaona et al., 2006; Méndez-Cárdenas and Zimmermann, 2009). In contrast to  
18  
19 Edwards' sportive lemurs, our study revealed that western woolly lemurs do not engage in  
20  
21 loud calling, duetting or chorusing behavior at resource sites. Thus, all in all these findings  
22  
23 suggest that the pattern of pair cohesiveness and/or phylogeny may influence divergence in  
24  
25 signaling behavior.  
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30 If phylogeny shapes vocal complexity then we would expect similarities in the size of  
31  
32 the vocal repertoire as well as in vocal behavior within the same taxonomic family despite  
33  
34 differences in activity pattern or social complexity. Indeed, acoustic signaling systems for  
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36 governing intra-group cohesion are functionally and structurally similar across members of  
37  
38 the same taxonomic family, the Indriidae. Thus, as our study reveals, the woolly lemurs use  
39  
40 the soft growling call and the loud whistle call for governing intra-group cohesion, dependent  
41  
42 on pair dispersion during foraging. The growling call is functionally and structurally similar  
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44 to the soft hums reported for indris and the soft grumbles for sifakas, which function to hold  
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46 contact with other group members at short distance (Pollock, 1975; Petter and Charles-  
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48 Dominique, 1979; Macedonia and Stanger, 1994; Maretti et al., 2010; Patel and Owren,  
49  
50 2012). Loud howl calls, comparable in their function to the loud whistle call in woolly lemurs,  
51  
52 are described for sifakas and indris and are given when an individual loses visual contact to  
53  
54 the group (Maretti et al., 2010; Patel and Owren, 2012; Torti et al., 2013). Loud calling in the  
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56 context of spacing between pairs is present across all studied taxa of the Indriidae. However,  
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3 as revealed in our study, only one pair partner emitted loud two-component avahee calls  
4 across the non-core areas of the home range, and these were answered with the same type of  
5 call, most likely by a neighbor. In contrast, in the diurnal pair-living indris and group living  
6 sifakas, both pair partners/all adult and subadult group members engage in loud duetting or  
7 chorusing (simultaneous calling of all group members), in particular at resource sites at the  
8 beginning of their activity (Pollock, 1986; Thalmann et al., 1993; Maretti et al., 2010; Fichtel  
9 and Kappeler, 2011; Patel and Owren, 2012). Songs in indris consist of nine different call  
10 types/notes/syllables, which can also be used context-specifically (Maretti et al., 2010; Torti  
11 et al., 2013). Certain syllables of the choruses of sifakas and the duets/choruses of indris such  
12 as the roars may also function as loud alarm calls for advertising the detection of disturbances  
13 or predators (e.g. Patel and Owren, 2012; Torti et al., 2013). Consequently, our results in  
14 combination with the literature does not support either the phylogenetic hypothesis or the  
15 social complexity hypothesis since indri and woolly lemurs, which exhibit the same social  
16 pattern, but differ in activity mode, also differ in the complexity of vocal signaling systems  
17 for intergroup spacing. All in all, these findings suggest that primate vocal complexity is  
18 driven by a mixture of at least three different factors, the degree of social cohesiveness,  
19 activity and phylogenetic history.  
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### 43 **Conclusion and areas for future research**

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45 This study provides first quantitative information on the role of acoustic  
46 communication for spacing and cohesiveness in the nocturnal western woolly lemur. As in  
47 diurnal socially cohesive strepsirrhine as well as haplorrhine primates, acoustic signaling  
48 represents an important mechanism to regulate distances within pair partners and between  
49 pairs in space.  
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56 Future bioacoustic studies with satellite and audiocollars allowing for simultaneous  
57 recordings of pair partners are now needed to better understand the role of multimodal  
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3 signaling for governing inter-group spacing as well as coordination and decision making  
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5 within woolly lemur groups. Such studies should be complemented by playback experiments,  
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7 in order to explore to which extent woolly lemurs use and perceive messages acoustically  
8  
9 conveyed in their calls. Furthermore, as loud calls are often used successfully to assess  
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11 taxonomic and phylogenetic relations or migrations patterns in primates (e.g. Zimmermann,  
12  
13 1990; Davila Ross and Geissmann, 2007; Méndez-Cárdenas et al., 2008; Meyer et al., 2012),  
14  
15 the role of loud calls in examining endangered woolly lemurs species diversity and evolution  
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17 as well as the conservation potential of loud calls (e.g. in studying species presence and  
18  
19 abundance) would merit specific attention.  
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23 Altogether, our study provided the first empirical research on the vocal signaling  
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25 system of the western woolly lemur as model for the hitherto neglected nocturnal, cohesive  
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27 pair-living primates. Our results emphasize the effect of the degree of social cohesiveness,  
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29 activity and phylogenetic history on the evolution of signaling systems and contribute to a  
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31 better understanding of the evolutionary roots of primate vocal communication.  
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46  
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48  
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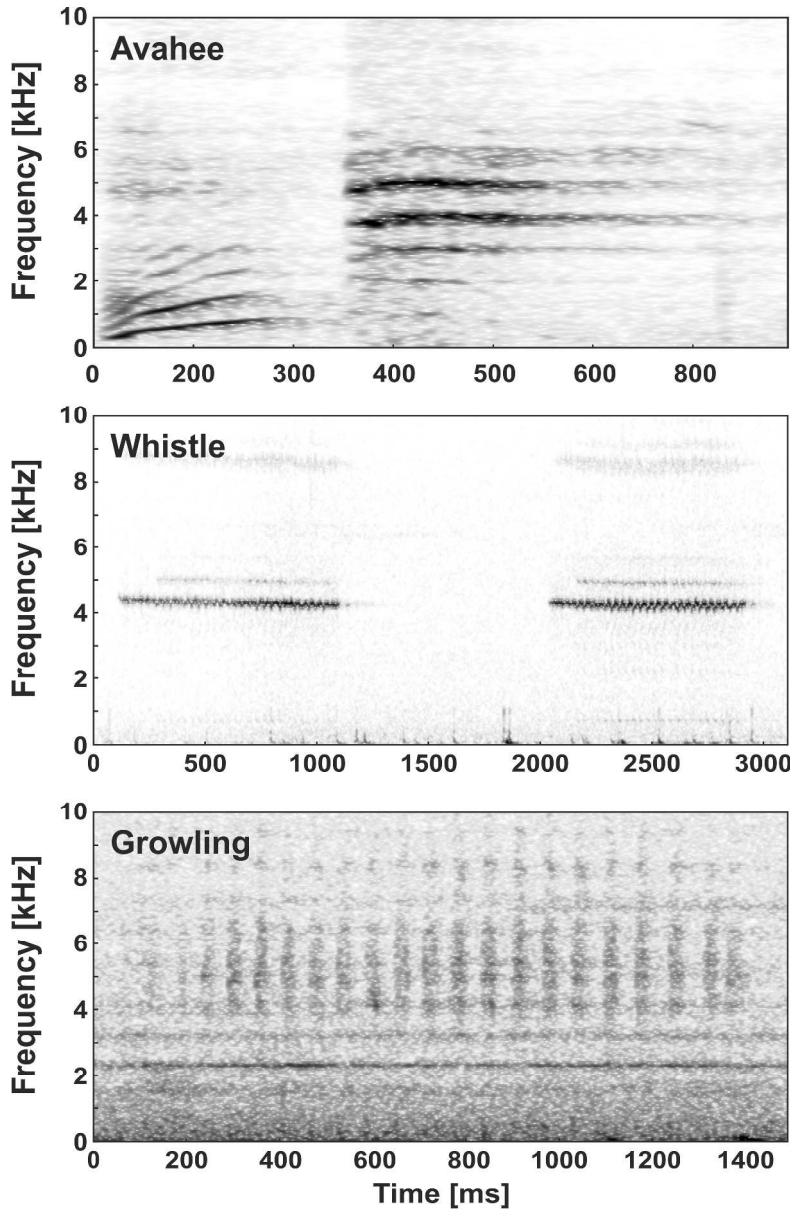
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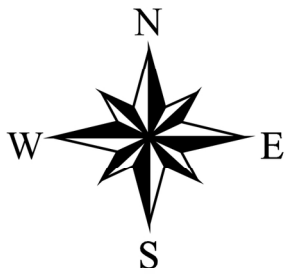
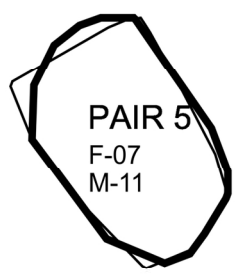
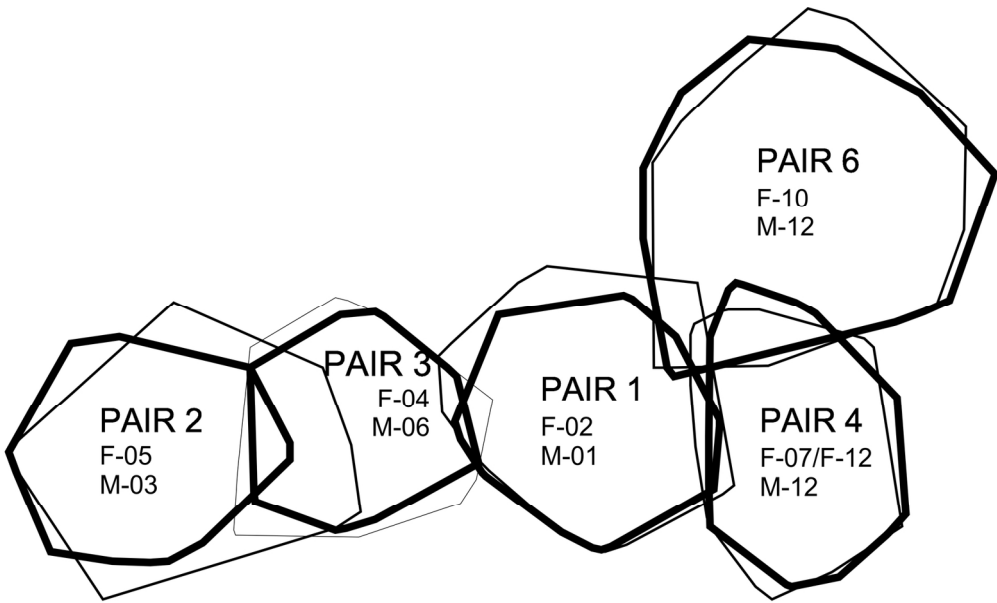
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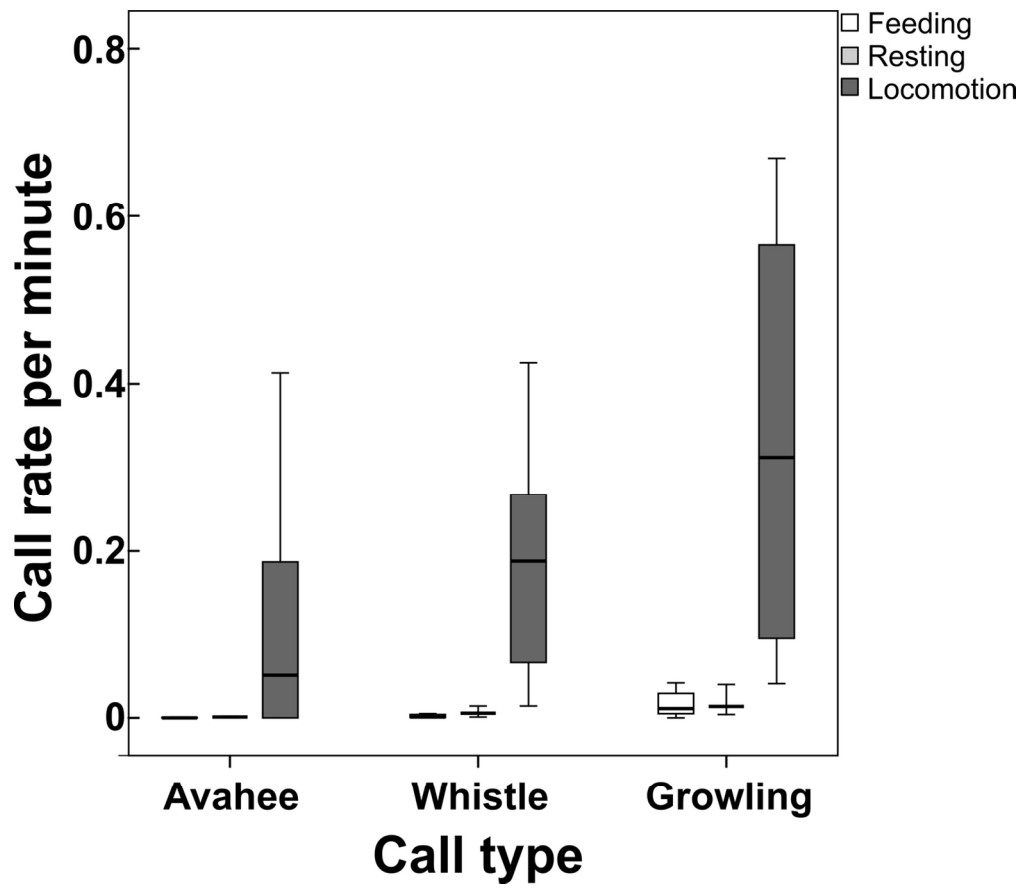
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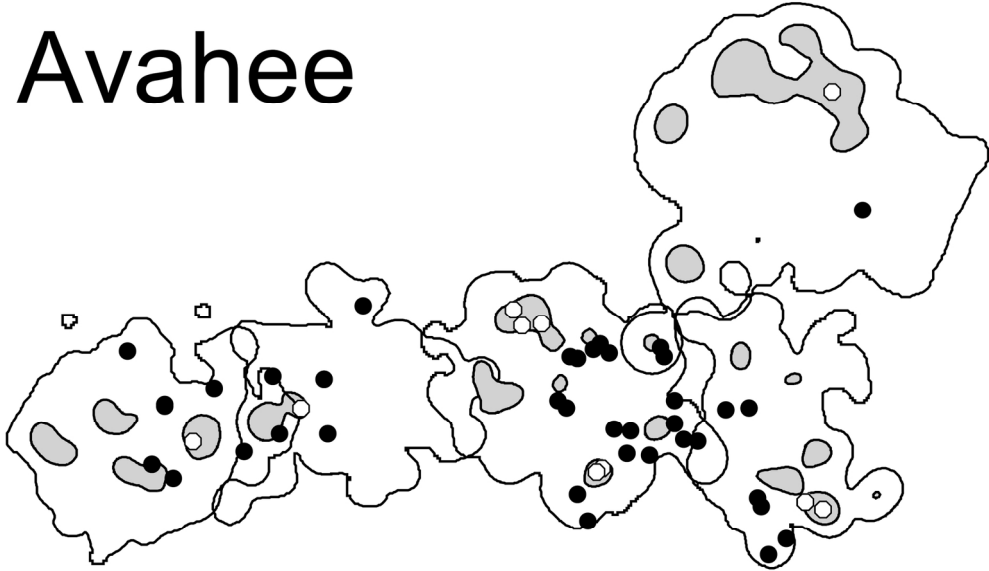


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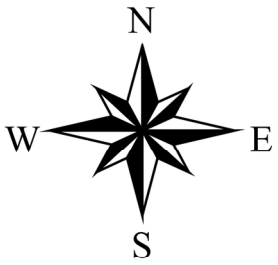
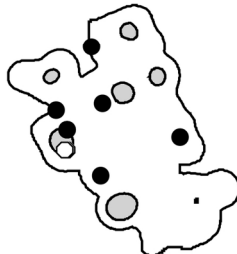


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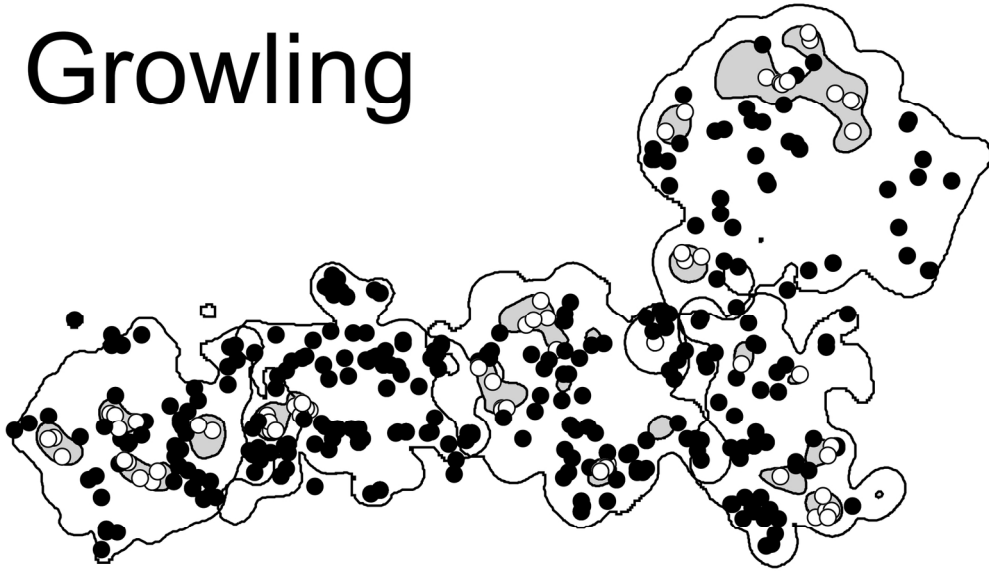
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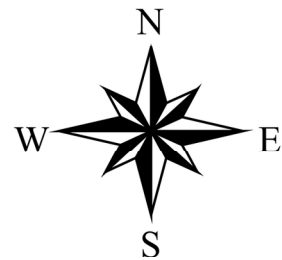
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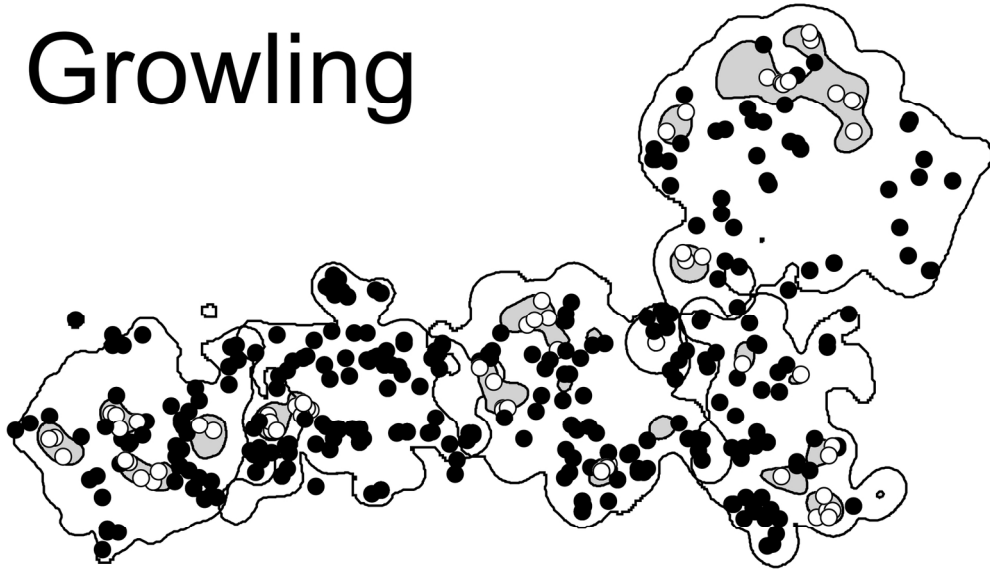
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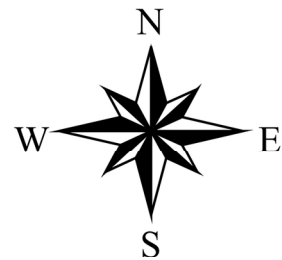
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