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Home Range Size and Social Organization of the Sahamalaza Sportive Lemur, *Lepilemur sahamalazensis*

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Abstract: Knowledge of a species' social organization and spatial needs is essential to set up effective conservation measures. To date, there have been published studies on the home range size and social organization of only three of the 26 sportive lemur species currently recognized; there is no information available for the remaining 23. We studied home range size and social organization for the first time in the Critically Endangered Sahamalaza sportive lemur (*Lepilemur sahamalazensis*) by following eight radio-tagged individuals for 666 hours. Observations were made at night, recording interactions between them and the distances they travelled. Home ranges covered 0.38 ha and there was no overlap between adult individuals; nightly ranges were about 0.1 ha. Almost no social interactions were seen, and the very few observed sociopositive interactions took place between mother and kin, as suggested by size differences and diurnal observations. The small number of individuals observed makes conclusive inferences about the social organization of *L. sahamalazensis* difficult to make, but the low level of social interaction and cohesiveness shown indicates little social complexity and the possibility that they are essentially solitary.

Key Words: Critically Endangered, home range, *Lepilemur*, sociality, spatial needs, sportive lemur

Introduction

Following socioecological models, the distribution of animals in time and space is related to the distribution of restricted resources (Emlen and Oring 1977; Clutton-Brock 1989). Restricted resources for females (for example, food and safe sleeping sites) affect offspring survival, while the key resource for males is access to fertile females. The distribution of the different limiting resources, therefore, is believed to be associated with group size and movement patterns (Trivers 1972; Clutton-Brock and Parker 1992; Wrangham *et al.* 1993; Dunbar 1994). Females should only tolerate males (with whom they compete for food) if they profit from a permanent association with them (for example, by their defense of territories against rivals, by protection from infanticide, or by cooperation in parental care; see van Schaik and van Hooff 1983; van Schaik and Kappeler 1997). Site-related territoriality may evolve if feeding sites or safe sleeping sites are distributed in a manner that makes them defensible (Kaufmann 1983).

The size of a species' home range varies according to body mass, diet, sex, and age, and is also related to season, population density, group size, weather variables or habitat degradation and fragmentation (Burt 1943; Clutton-Brock and Harvey 1979; Harestad and Bunnell 1979; Haskell *et al.* 2002; Singh *et al.* 2001). Primate groups tend to be smaller and densities lower in secondary forests than in primary forests (Donati *et al.* 2011; Estrada and Coates-Estrada 1995; McCann *et al.* 2003; Schwitzer *et al.* 2007b). This suggests that a larger home range is necessary to sustain the same number of individuals in a secondary forest, and in the case of the lemurs this is most likely because larger home ranges are necessary for them to find sufficient food resources (Clutton-Brock and Harvey 1979; Robbins *et al.* 2006). Primate species that are ecologically flexible will be less affected by the loss of original habitat than those that rely on specific habitat characteristics or food resources present only in certain forest types (Andrianasolo *et al.* 2006; Ganzhorn and Schmid 1998; Schwitzer *et al*. 2007b).

The diversity of social systems of nocturnal prosimians is still not fully understood (Kappeler and van Schaik 2002). While some nocturnal species are pair-living, most appear to live in more complex societies where they rest in pairs or groups during the day but forage alone during the

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night (Charles-Dominique 1977; Müller and Thalmann 2000). A number of species previously thought to be solitary are in fact pair-living (Fat-tailed dwarf lemur *Cheirogaleus medius*: Fietz 1999; Milne-Edwards' sportive lemur *Lepilemur edwardsi*: Thalmann 2001; Masoala fork-marked lemur *Phaner furcifer*: Petter *et al.* 1971; Schülke and Kappeler 2003; and Western woolly lemur, *Avahi occidentalis*: Thalmann 2003). It seems, however, that most nocturnal pair-living species differ in their degree of cohesiveness from diurnal pair-living primate species because males and females are only loosely associated (Müller and Thalmann 2000; Schülke and Kappeler 2003). In contrast to cohesive pairs that have frequent grooming bouts, small inter-individual distances and close coordination of the behavior of male and females (Müller and Anzenberger 2002), the "dispersed pairs" share the same home-range but are not continuously associated during their period of activity (for example, the Masoala fork-marked lemur*:* Schülke and Kappeler 2003). As dispersed pairs combine aspects of the likely evolutionary change of a solitary social organization to pair living, they may represent the earliest and most primitive form of sociality (Dröscher and Kappeler 2013).

The first field studies concluded that the typical mating system of solitary prosimians is most likely spatial polygyny; an adult male has access to the ranges of several females (Charles-Dominique 1977; Bearder 1987). More recent studies have identified other forms of polygyny (Kappeler 1997a; Eberle and Kappeler 2002). Müller and Thalmann (2000) concluded that the dispersed multimale-multifemale system and dispersed pair-living are the predominant patterns for solitarily foraging nocturnal primates and that dispersed harems (i.e., spatial polygyny) occur only seldom.

All sportive lemur species are now categorized as Vulnerable (4), Endangered (18) or Critically Endangered (4) on the IUCN Red List (Davies and Schwitzer 2013; IUCN 2014). The Sahamalaza sportive lemur is Critically Endangered (Davies and Schwitzer 2013; IUCN 2014), and was included on the list of the World's Top 25 Most Endangered Primates 2006–2008 (Olivieri *et al.* 2007a). The Sahafary sportive lemur, *L. septentrionalis*, occurring in far northern Madagascar, has been on the list of the World's 25 Most Endangered Primates since 2008. Despite this, home range size and social organization have been described for only three of the 26 currently recognized species. Zinner *et al.* (2003) found that male and female red-tailed sportive lemurs (*Lepilemur ruficaudatus*) occupied small home ranges (0.8 ha, 95% Kernel probability plots) that were stable over several years. While they form territorial pairs, the pair met only rarely except during the short mating seasons, and Hilgartner (2006) classified them as living in dispersed pairs. Milne-Edwards' sportive lemurs have similar home range sizes (Albignac 1981), but 3–4 individuals can often be seen feeding, without aggression, in the same tree, moving together for several hours, and grooming each other (Warren 1994). The mean home range size of females was recorded as 1.1 ha (Minimum Convex Polygons, MCP; Albignac 1981), with considerable home range overlap. According to Thalmann (1998), Milne-Edwards' sportive lemurs live in dispersed family groups and are possibly pair-bonded. In a more recent study, it was described as pair-bonded, with the formation of stable sleeping associations between pair partners during the day and exclusive sleeping site and home range use (Rasoloharijaona *et al.* 2003, 2006). Reported mean home range size (MCP) was 0.98 ± 0.4 ha for females and 1.01 ± 0.25 ha for males (Rasoloharijaona *et al*. 2006).

In studies of the white-footed sportive lemur (*L. leucopus*), most of the social units were found to be dispersed pairs, but some males were associated with two adult females (Charles-Dominique 1971; Dröscher and Kappeler 2013). According to Hladik and Charles-Dominique (1974) and Russell (1977), adult females defend a territory of about 0.18 ha, and adult males defend territories of about 0.30 ha. Grooming and the sharing of sleeping sites were not observed in these studies, and interaction tests even indicated active avoidance between pair partners (Dröscher and Kappeler 2013). There is no data for any other sportive lemur species.

Here, we report on our observations of home range size and social organization in the Sahamalaza sportive lemur, *Lepilemur sahamalazensis*. It is believed to be restricted to the Sahamalaza Peninsula in northwestern Madagascar (Olivieri *et al.* 2007b), an area that has experienced rapid and widespread deforestation. *Lepilemur* density in the Ankarafa forest, one of the three remaining forests in the species' distribution, ranged from 0.07 to 0.23 ind/ha (Seiler *et al.* 2013b). The smallest fragment where they occurred measured 10 ha.

In our earlier studies regarding their choice and use of habitats at night and in the daytime, we found that the lemurs actively chose sleeping sites and used home ranges according to habitat parameters that included high tree density, high level of canopy cover, and abundance of feeding trees and sleeping site trees (Seiler *et al*. 2013a, 2014). During the day, the lemurs rested alone in tree holes or dense tangles of vegetation up in the trees ("tree tangles") (Seiler *et al.* 2013a). Only mothers and babies (<2 months old) and mothers and infants (siblings from the previous year, <1 year) were observed to share sleeping sites. They were active for 5–14% of the daytime—autogrooming, being vigilant, and moving about—but never left their sleeping sites or fed. Owing to their exposed resting positions, these lemurs were easily accessible to diurnal predators, such as the Madagascar harrier hawk (*Polyboroides radiatus*), the fossa (*Cryptoprocta ferox*), and possibly the Madagascar tree boa (*Sanzinia madagascariensis)*, as well as to human hunters (Seiler *et al.* 2013a).

An understanding of the species' social organization and spatial needs is crucial for an assessment of the habitat needs of this rare lemur, and furthermore might support conservation measures for all sportive lemurs. On the assumption that the home range would be similar in size to those of other sportive lemurs, we expected that *L. sahamalazensis* would use home ranges of approximately 1 ha. The likelihood was also that they are dispersed pair-living animals defending exclusive territories, and as such we expected to find home range overlap between certain adult male and female individuals and

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minimal, if frequent, social interactions during their activity time. This would indicate similar-sized home ranges for males and females.

Methods

Study site

Ankarafa Forest is in the UNESCO Biosphere Reserve and national park on the Sahamalaza Peninsula, in the Sofia Region, northwest Madagascar (Fig. 1). It extends between 13°52'S and 14°27'S and 45°38'E and 47°46'E. The climate is strongly seasonal, with a cool, dry season from May to October and a hot, wet season from November to April. Ankarafa Forest lies in a transition zone between the Sambirano domain in the north and the western dry deciduous forest domain in the south. The forest is semi-humid with tree heights of up to 25 m (Schwitzer *et al.* 2006).

There are no large areas of intact primary forest left on the Sahamalaza Peninsula, and the remaining fragments all show some degree of anthropogenic disturbance and edge effects (Schwitzer *et al.* 2007a, 2007b). The forest fragments are separated by grassland with shrubs. Besides *L. sahamalazensis*, the lemur community in Sahamalaza includes the blue-eyed black lemur *Eulemur flavifrons*, aye-aye *Daubentonia madagascariensis*, northern giant mouse lemur *Mirza zaza*, Sambirano lesser bamboo lemur *Hapalemur occidentalis*, and the fat-tailed dwarf lemur *Cheirogaleus medius*. All are threatened by hunting and forest destruction (Schwitzer *et al.* 2006). To date, the Sahamalaza sportive lemur has been confirmed only for this area.

Behavioral observations

Eight Sahamalaza sportive lemurs (seven females, one male) living in four forest fragments were fitted with radio-collars and followed during two field seasons (July–October 2009; April–August 2010). Mating activity has been described for the red-tailed sportive lemur (Hilgartner 2006) and Milne-Edwards' sportive lemur (Randrianambinina *et al.* 2007) as occurring in May and June, and we believed our field season would include the mating season of the Sahamalaza sportive lemur. We were unable to find further individuals that we were able to collar. The sportive lemurs were captured during the day at their sleeping sites (tree hole or tree tangle) with a blowpipe, using 1-ml, cold air-pressure, narcotic

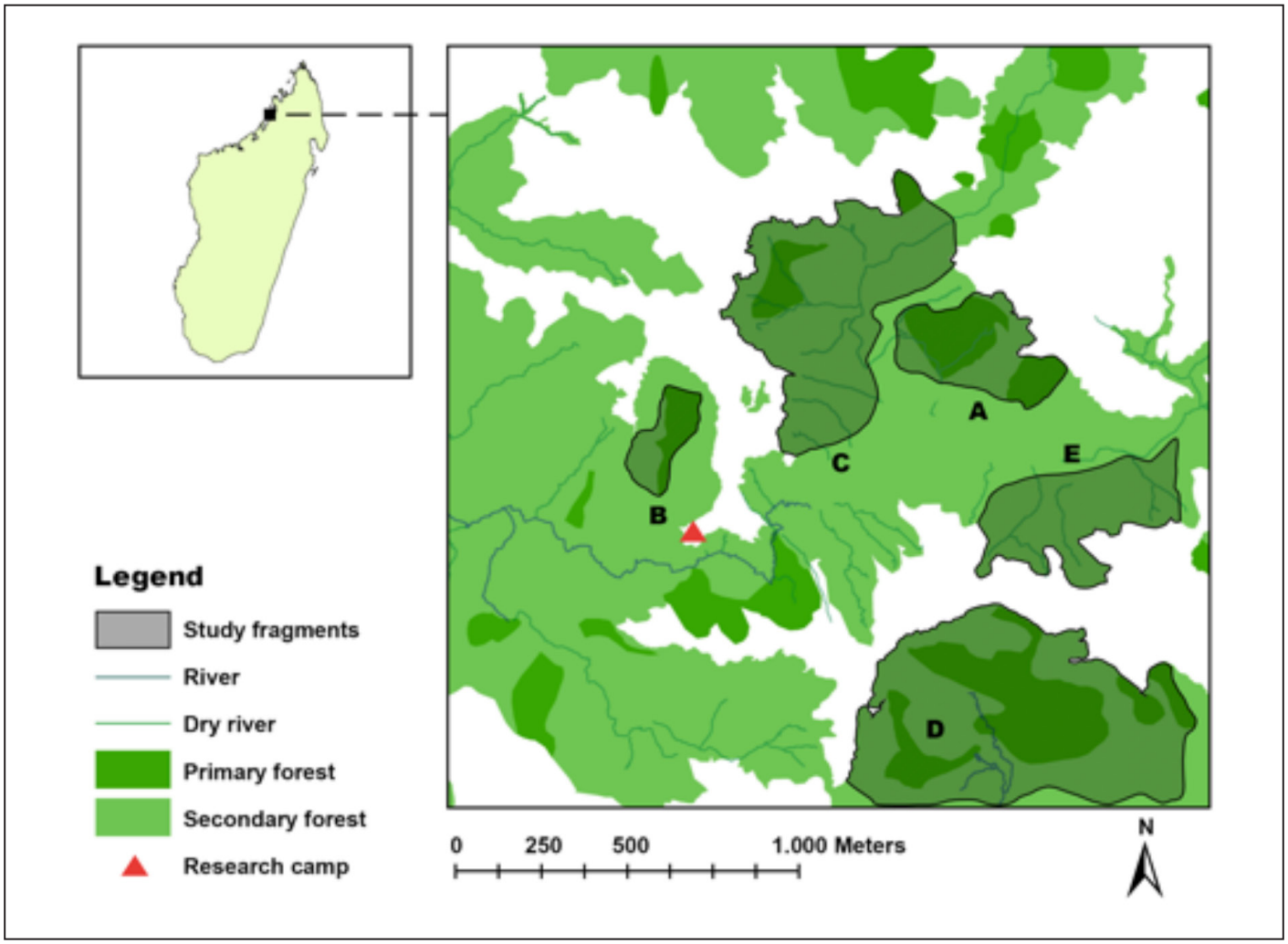


Figure 1. Study fragments (A–E) and the location of the research camp in the Ankarafa Forest, Sahamalaza Peninsula, northwest Madagascar. Fragments C and A are separated by a swamp, and low secondary growth (bushes, saplings) separate the other fragments.

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syringe projectiles from Telinject (Römerberg, Germany). Lemurs were anesthetized for a short time to take body measurements (see Table 1) and equip them with radio collars. We used Ketasel 50 (50 mg Ketasel/ml) in the dose recommended by the manufacturer (0.01 ml/100 g body mass), but we had to increase the dose to 0.03 ml/100 g for three of the animals (large females). They were released after recovery at their capture site at the onset of their activity period. The animals captured were identified as adults by their body measurements and tooth profile.

In the first field season, TW3 brass-collar tags (Biotrack, Dorset, UK) were used. Smaller TW3 button cell collars (Biotrack, Dorset, UK), attached with cable ties for better adjustment, were used in the second field season. To make sure that the behavior of the collared individuals was not altered due to the collar, we observed five of them during the day (180 observation hours) and tested their levels of activity against the level of activity of un-collared individuals (N = 40, 1200 observation hours). There were no significant differences (Wilcoxon signed-ranks test: df = 45; Z = -0.943; P = 0.864). The radio collars were removed at the end of each field season, and most animals had gained weight compared to the first time we captured them (see Table 1), indicating that they were not agitated or disadvantaged by wearing them.

During night observations (18:00–06:00), the radio-collared lemurs were followed using a portable TR-4 receiver (Telonics; Mesa, Arizona, USA) during the first season, and a Biotrack receiver in the second season, a three-element yagi antenna (Biotrack, Dorset, UK) and a GPS device (GPS 60; Garmin Ltd., Schaffhausen, Switzerland). A new GPS location was logged every time the individual being followed moved to another location. If animals rested in one location for a prolonged period of time, only one GPS data point was logged. We preferred this method to a periodical logging of location points as it was not always possible to locate an individual at all times. We conducted analyses of home range size and location via MapSource (version 6.13.7; Garmin Ltd., Schaffhausen, Switzerland). We estimated the overall home range per individual (N = 8) via 95% minimum convex polygons using all the location points of nocturnal follows per individual (Table 1). The method creates a polygon including all the locations where an individual was recorded (Mohr 1947), and it is possible that it calculates a larger home range when compared to Kernel density estimations. Most studies describing primate home range size use the MCP method, and we have used it to compare our results with those obtained for other species. To present a more detailed picture of the individuals' home ranges, we present the range sizes for each night in addition to the overall home range size.

Social behavior (recorded as instances of allogrooming, body contact, and agonistic behavior) and estimated distances to other sportive lemurs (if less than 15 m) were recorded continuously using focal animal sampling (Altmann 1974). "Near other" was also noted when the focal individual was out of sight but its location was known (for example, animal out of sight in the canopy of a large tree). We chose this method to avoid missing especially brief behaviors that are easily overlooked when using an interval observation method. In total, we followed the eight individuals at night for 666 hours (Table 1).

Data analysis

For comparisons of ranges covered during each observation night, we used a non-parametric Kruskal-Wallis ANOVA.

Table 1. Body measurements (cm) and capture details of eight radio-collared adult *Lepilemur sahamalazensis*.

Individual	1	2	3	4	5	6	7	8
	Male	Female	Female	Female	Female	Female	Female	Female
Body mass (g) at first capture	675	760	554	810	835	700	712	648
Head & body length	26	26	25	26.5	28	28,5	26	27
Tail	27.5	24	26	26.7	29	26	23	23.5
Nose-hindhead	5.5	5.47	5.27	5.2	6.09	5.42	5.9	5.87
Between ears	3.5	3.45	3.36	3.5	3.26	3.18	3.5	3.68
Femur	10.3	10.5	9	9.5	10.5	9	9	11
Tibia	10.6	10.5	10	10	10.5	10	10	10
Foot	7.7	6.8	7	6.8	8	7	7.2	7
Upper arm	6.2	6.5	5	7.5	6	6	7	6.5
Forearm	6.6	6.5	6.5	7.1	6	7	7	7
Hand	5	4	5	4.5	5.5	5.5	5	5.5
Weight of collar (g)	20	5	5	20	5	5	5	5
Study fragment	C	C	C	A	D	D	B	B
Capture date	3 Aug 09	15 May 10	17 May 10	3 Aug 09	18 May 10	19 May 10	14 May10	15 May10
Total night follows	11	5	6	11	6	6	4.5	6
Observation time (h)	132	60	72	132	72	72	54	72
Waypoints	987	438	701	1025	579	663	345	512
Out of sight (%)	74	46	32	69	46	28	33	47
Date of recapture	6 Jan 10	23 Sep 10	3 Jun 10	7 Jan 10	4 Jan 11	4 Jan11	5 Jan 11	3 Jun 10
Body mass (g) at recapture	702	782	538	874	834	715	762	639

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When differences between individuals were statistically significant, we applied multiple Mann-Whitney-U tests with Holm's Sequential Bonferroni corrections as *post hoc* tests. The significance level α was chosen as 5% ($P \leq 0.05$). Statistical tests were carried out using SPSS 19.0 (SPSS Inc., Chicago, USA). As social interactions were very rare, we give an overview of the average number of interactions per hour but forego statistical comparisons.

Results

Ranging behavior

The lemurs had a median home range of 0.38 ha (Table 2; Fig. 2). The range covered in one night was 0.1 ha. There were no significant differences in range sizes covered in one night between the females, but the night range of the male was significantly larger than those of five of the females (Table 2). The largest home range was found for L5 (Table 2; Fig. 2); a female that rested in a tree hole or tree tangle on one side of a canyon during the day, which she would cross to spend the night on the other side of it, before returning to her sleeping site in the morning. But the variation in night ranges of female L5 were similar to those of the other females.

Social behavior

Home ranges of the collared individuals did not overlap (Fig. 3), but during night observations other, non-collared, individuals were occasionally spotted in the home ranges, indicating that individuals do overlap in their home ranges. Sometimes sportive lemurs were observed to be near (distance <15m) other sportive lemurs, but usually they did not interact (Table 3). In two cases, we saw sociopositive contact with another individual. On both occasions, the individuals approached each other and licked each other's faces. One of these meetings was between the collared male and a larger female; the other between females of different sizes, which we think may have been a mother and daughter, as the collared female rested close to the other, smaller female during the day. Agonistic behavior towards other individuals—chasing other individuals without physical contact—was observed once for five, and twice for one of the eight lemurs (Table 3). Female L4 was observed to hit out towards another individuals' face with her hands when another individual approached the tree in which her baby was situated until the second individual fled. Body contact with allogrooming was observed only by mothers with their infants during diurnal observations, and is not considered here (see Seiler *et al.* 2013a). Five of the seven collared females had babies, born between mid-September and early October. We never observed any mating activity.

Discussion

Our preliminary results suggest that the observed Sahamalaza sportive lemurs have a low social complexity and might be solitary. They had exclusive territories of 0.38 ha with relatively small ranges of 0.1 ha per night and showed very little social interaction, probably largely between mother and kin.

Established home ranges might be important to minimize energy expenditures, which, being small folivores, might be of great importance to sportive lemurs (Kay 1984). During its resting period, *L. ruficaudatus* was found to have a markedly reduced metabolic rate (only 40% of the Kleiber value; Drack *et al.* 1999), probably to minimize energy expenditure (Ganzhorn 2002). It remains unclear if all sportive lemur species have a reduced metabolic rate during the day, especially when they are awake during their resting period, or if the metabolic rate is also reduced during their active period at night. Energy-saving strategies for the activity period should

Table 2. Home range size and median range per night (with quartile 1 and quartile 3) of eight *Lepilemur sahamalazensis* (L). Medians with different superscripts within a column differ significantly (Mann-Whitney U-tests with Holms-Bonferroni-Correction after Kruskal-Wallis ANOVA with α=0.05). Medians for all sportive lemurs are given in the last row.

Individual	L1	L2	L3	L4	L5	L6	L7	L8	ANOVA	Median
Home range (ha)	0.72	0.25	0.42	0.35	4.04	0.54	0.18	0.23		0.38 (0.27-0.59)
Nightly range (ha)	0.27^{a} (0.17-0.37)	0.12^{ab} (0.12-0.15)	0.07^{b} (0.03-0.09)	0.1^{b} (0.07-0.13)	0.05^{b} (0.02-0.11)	0.19^{ab} (0.1-0.22)	0.04^{b} (0.04-0.05)	0.09^{b} (0.06-0.09)	P=0.003, df =7 χ^2=21.868	0.1 (0.06-0.18)

Table 3. Total observation hours, hours in sight and amounts of social contacts of eight *Lepilemur sahamalazensis* (n/h with total numbers, for *Near other* based on total observation time, for further social behavior based on time in sight).

	Observation time (h)	In sight (h)	Near other (<15m)/h (total time)	Body contact/h (when in sight)	Agonistic/h (when in sight)	Allogrooming/h (when in sight)
L1 (male)	132	34.32	0.06 (8)	0.03 (1)	0.03 (1)	0.03 (1)
L2 (female)	60	32.4	0.09 (7)	0	0.03 (1)	0
L3 (female)	72	48.96	0.019 (9)	0	0.02 (1)	0
L4 (female)	132	40.92	0.19 (14)	0	0.02 (1)	0
L5 (female)	72	38.88	0.08 (6)	0	0	0
L6 (female)	72	51.84	0.18 (13)	0.02 (1)	0.03 (2)	0.02 (1)
L7 (female)	54	36.18	0.22 (16)	0	0.03 (1)	0
L8 (female)	72	38.16	0.1 (4)	0	0	0

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nonetheless also be important for sportive lemurs and were found in a former study of *L. sahamalazensis* by Seiler *et al.* (2014). Energy saving might also explain the relatively small home ranges of sportive lemurs—about 1 ha for *L. edwardsi* (see Albignac 1981; Warren and Crompton 1997) and *L. ruficaudatus* (Zinner *et al.* 2003), and 0.18 ha for female and 0.33 ha for male *L. leucopus* (see Dröscher and Kappeler 2013). The much smaller grey mouse lemur (*Microcebus murinus*), with its broad diet, has similar home ranges of 0.7–1.6 ha for females and 2.8–4.8 ha for males in dry deciduous forest (Eberle and Kappeler 2004; Lahann 2008; Radespiel 2000). With a median size of 0.38 ha, the home ranges of the Sahamalaza sportive lemurs we observed were similar in size to those found for the white-footed sportive lemur (Dröscher and Kappeler 2013). The animals only covered an average area of 0.1 ha in their home ranges during any one night. In our study, the only male animal in our sample covered a significantly larger range per night (0.27 ha) than did the females (0.09 ha).

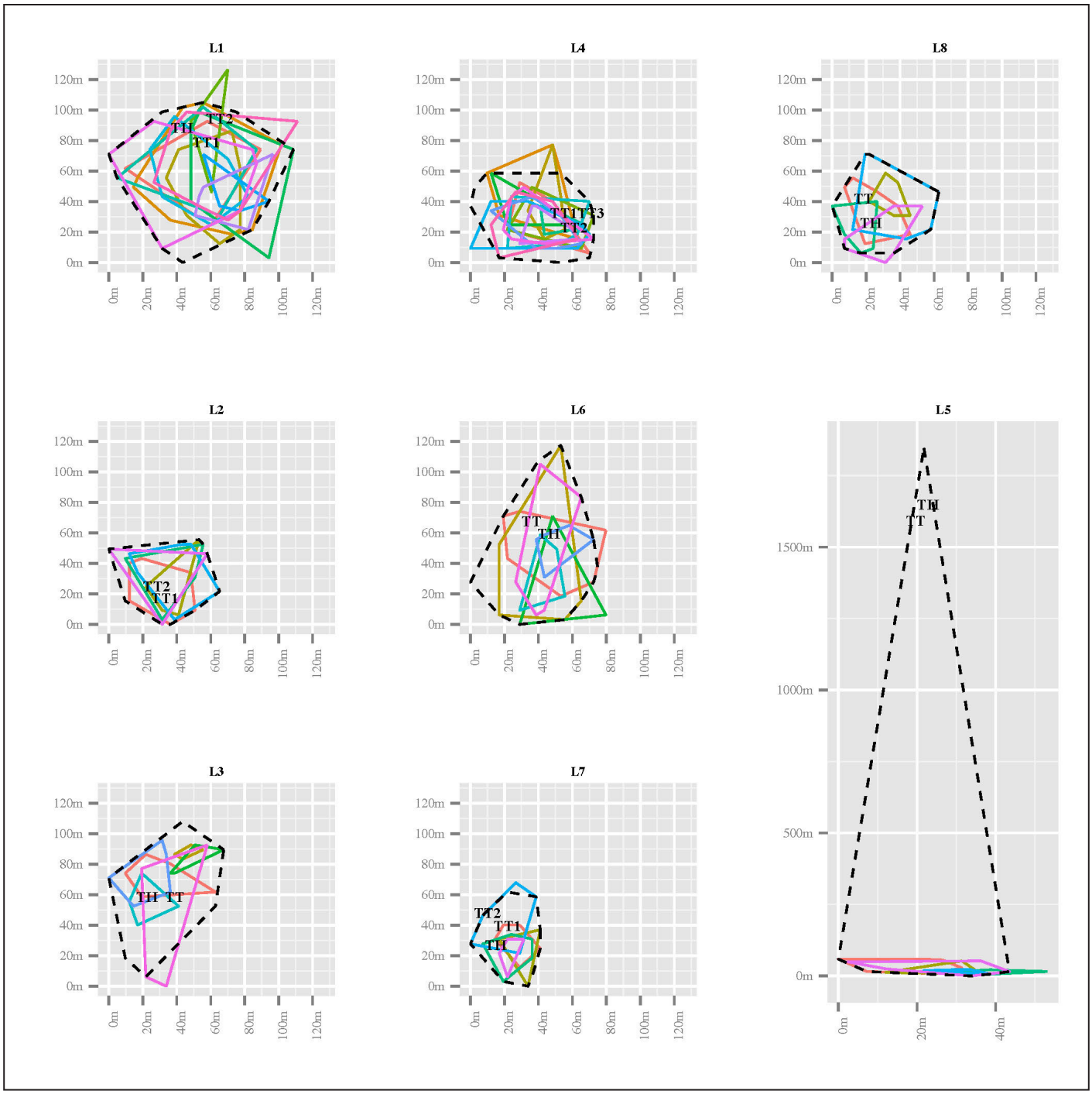


Figure 2a. Home ranges of seven females (L2−L8) and one male Sahamalaza sportive lemur (L1) during nocturnal observations. TH = tree hole, TT = tree tangle. Different colors mark the individual's home ranges on different nights. The overall home ranges are marked by dashed lines.

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Because our observations were limited to just one male, we are unable to draw any firm conclusions concerning the social organization of *L. sahamalazensis*. The differences in night ranges between the male and the females could point towards a polygynous mating system, where adult males defend territories that cover those of 1–5 females, as has been described for *L. leucopus* by Hladik and Charles-Dominique (1974). Most of the social units of *L. leucopus* were found to occur in dispersed pairs, while some males were also associated with two adult females (Charles-Dominique 1971; Russell 1977; Dröscher and Kappeler 2013). Dröscher and Kappeler (2013) found very little social contact and active pair avoidance between pair-partners, and also that home ranges of males were substantially larger than those of females (0.33 ha vs. 0.18 ha), suggesting polygyny. Dröscher and Kappeler (2013) concluded that "the low cohesiveness together with extremely low rates of social interactions places the white-footed sportive lemur at the low end of primate social complexity," a statement that is also true for our study on the Sahamalaza sportive lemur.

In general, we were able to observe individual sportive lemurs resting and feeding with relatively small distances between them, but social interactions were extremely rare and mainly agonistic (for example, chasing). The two allogrooming events we observed, most likely involved mother and offspring; one individual was slightly smaller than the other and we observed smaller individuals resting in proximity to the collared females that were known to have had offspring the previous year. In total, we observed 88 social interactions, including sitting separated by less than 15 meters. This was during 666 hours of night observations, resulting in only 0.15 social interactions per hour across all individuals. As we were not able to observe focal animals at all times during our night follows, this value should be considered as a minimum value and might be higher. However, this rate of observed social interactions is very similar to the 0.14 interactions/h across pairs recorded for *L. leucopus* by Dröscher and Kappeler (2013).

As individuals with little social contact may regulate their relationship with the help of vocal or olfactory signals, and

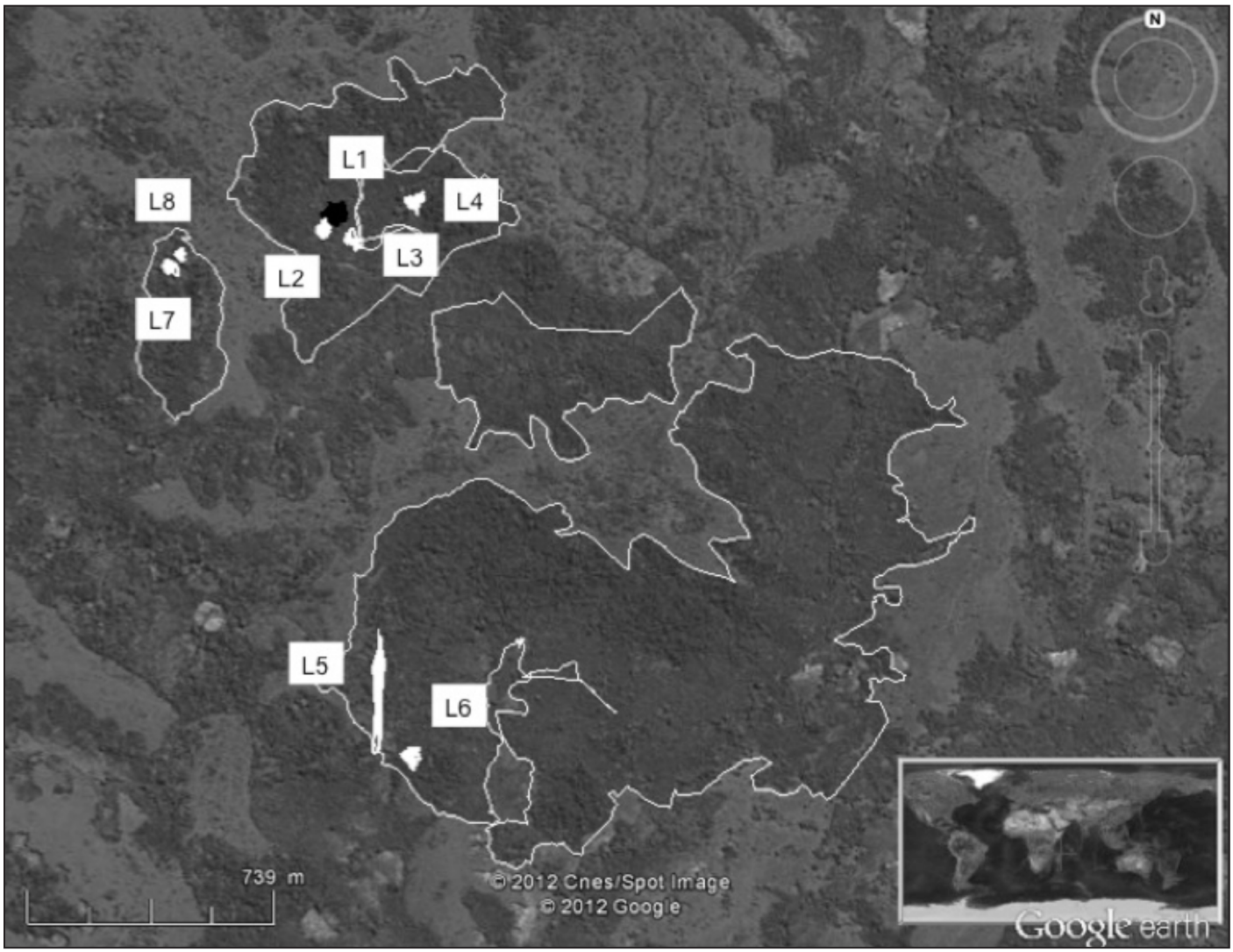


Figure 3. The home ranges of seven collared female (white) and one collared male (black) Sahamalaza sportive lemurs in relation to each other and the five forest fragments.

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home ranges of certain male and female individuals overlapped in their study, Dröscher and Kappeler (2013) concluded that the white-footed sportive lemur lives in dispersed pairs. Sportive lemurs have been described as highly vocal (Rabesandratana 2006; Rasoloharijaona *et al.* 2006), and the use of loud calls for coordinating pair movements has been described for the pair-living *L. edwardsi* by Rasoloharijaona *et al.* (2006) and Méndez-Cárdenas and Zimmermann (2009). *Lepilemur ruficaudatus* on the other hand exhibited only a low rate of mutual (but not coordinated) vocal exchanges between pair-partners, suggesting that loud calling serves as a territorial signal and to regulate spacing (Fichtel and Hilgartner 2012), similar to what we found for *L. sahamalazensis* in another part of our study (Seiler *et al.* 2015). *Lepilemur sahamalazensis* vocalized only rarely (0.2 calls/h), and had a similar number (6, potentially 7, Seiler *et al.* 2015) of distinct call types to other sportive lemurs: *L. edwardsi* (9 call types) Rasoloharijaona *et al.* (2006); *L. ruficaudatus* (6 call types) Fichtel and Hilgartner (2012); and *L. leucopus* (5 call types) Dröscher and Kappeler (2013). The most frequent calls are likely to be either territorial or related to mother-infant communication (Seiler *et al.* 2015). We did not observe glandular scent-marking (or any forms of scent marking) or branch-bashing displays such as those described for male *L. leucopus* by Dröscher and Kappeler (2013). We did observe individuals tree gouging when in their sleeping trees, resting. Tree gouging in weasel sportive lemurs (*Lepilemur mustelinus*) is thought to be used to register sleeping tree ownership (Rasoloharijaona *et al.* 2010). As this behavior often occurred after or during autogrooming in *L. sahamalazensis*, it is also possible that it is used to clean their mouth from hair.

Based on the very rare social interactions during the night, the solitary use of sleeping sites during the day, the low rate of loud calls, solitary use of home ranges and the lack of marking behavior, we believe that it is unlikely that the Sahamalaza sportive lemur is organized in dispersed pairs such as has been described for *L. ruficaudatus* and *L. leucopus* by Hilgartner (2006) and Zinner *et al.* (2003), respectively, or dispersed family groups with bonded pairs as in *L. edwardsi* (see Thalmann 1998). Our results rather point towards a solitary social system for the Sahamalaza sportive lemur, with home range overlap most likely only between relatives. In a solitary species "the general activity, and particularly, the movements of different individuals about their habitat are not synchronized" (Charles-Dominique 1978), resulting in solitary foraging of individuals (Bearder 1987) in contrast to gregarious animals, which synchronize their activity in space and time (Boinski and Garber 2000). Nonetheless, our data are not sufficient to draw definitive conclusions, and it is possible that more social interactions between adults during the night can be observed between November and early April, when we did not conduct observations.

As mating takes place in May and June in *L. ruficaudatus* and *L. edwardsi* (Hilgartner 2006; Randrianambinina *et al.* 2007, respectively), we assumed that the Sahamalaza sportive lemurs would also mate at this time. We never observed any mating. In the first field season, we were able to observe that babies are born in September, which is about a month earlier than described for the other sportive lemur species. Considering a gestation period of 4–5 months for sportive lemurs (see, for example, Hilgartner 2006), we thus considered that the mating season for the Sahamalaza sportive lemur should be in April–May and started the second field season in April, but were not able to observe mating or increased social activity during that time, either. This might mean that mating took place but we failed to observe it, or that the mating season for the Sahamalaza sportive lemur is even earlier in the year, which would mean that the gestation period would have to be longer than 4–5 months. Studies over an entire year are needed.

Generally, the close overlap of male and female ranges including territorial defense against neighbors in many nocturnal primates, such as *L. edwardsi* (Rasoloharijaona *et al.* 2000; Thalmann 2001), *L. ruficaudatus* (Hilgartner 2006; Zinner *et al.* 2003), the Zanzibar galago *Galagoides zanzibaricus* (see Harcourt and Nash 1986), *Cheirogaleus medius* (Fietz, 1999; Müller 1998), and the fork-marked lemur *Phaner* (Charles-Dominique and Petter, 1980; Schülke, 2003), that lack constant associations between the pair partners, are thought to be examples of independent transitions from a solitary to a pair-living social organization (Kappeler 1999c; Kappeler and van Schaik 2002). The Sahamalaza sportive lemur might represent a very primordial example of social organization in primates.

The advantage of a solitary life style for the Sahamalaza sportive lemur, especially of resting alone during the day, could be explained by the high predation pressure in their non-activity time and their sophisticated anti-predator behavior. The Sahamalaza sportive lemur shows considerable vigilance during the day, and listens to calls of surrounding species as well as predator vocalizations to react rapidly depending on the threat. By resting alone and freezing or fleeing into a tree hole, it minimizes the chances to be spotted by a predator (Seiler *et al.* 2013a). As a rather generalized herbivore feeding on at least 42 different and abundant tree species (Seiler *et al.* 2014), individuals should also not need a pair partner to help defend their food resources (resource defense theory; Brockelman and Srikosamatara 1984). Furthermore the paternal care hypothesis that assumes that the reproductive success of the female would suffer without help of a pair partner (Kleiman 1977; Clutton-Brock 1989) can be discarded for the Sahamalaza sportive lemur, as no male was ever spotted around mothers with youngsters or the youngster when left in a tree during the night (M. Seiler, pers. obs.). For the same reason, we can discard the infanticide-avoidance hypothesis, which assumes that infanticide is the primary force selecting for males associating permanently with one female unable to defend their infants against strange males (see, for example, van Schaik and Kappeler 1997). Seiler *et al.* (2015) reported that the observed female *L. sahamalazensis* with babies rapidly moved towards the tree that their babies were in when presented with the call type "2-parts", a possible mating call

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of the species. We argued that it is possible that females will aim to avoid unknown males during the offspring care period. A case of infanticide at the onset of the offspring care period has been described for *L. edwardsi* by Rasoloharijaona *et al.* (2000). These observations suggest that females might indeed profit from a pair partner for infant protection, but our preliminary observations do not support that this is the case in the Sahamalaza sportive lemur.

Our results suggest that the Sahamalaza sportive lemur copes with this low energy diet by having relatively small home ranges. Though we cannot finally confirm this assumption, *L. sahamalazensis* might be the first-described solitary species in the genus *Lepilemur*.

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