

RESEARCH ARTICLE

Use of space and home range characteristics of *Lepilemur mittermeieri*, an endangered sportive lemur endemic to the Ampasindava peninsula, north-west Madagascar

Leslie Wilmet^{1,2}  | Roseline C. Beudels-Jamar² | Christoph Schwitzer³ |
Hajanirina Rakotondrainibe⁴ | Pierre Devillers² | Cédric Vermeulen¹

¹TERRA Research Center, Forest is Life, Gembloux Agro-Bio Tech - University of Liège, Gembloux, Belgium

²Conservation Biology Unit, OD Nature, Royal Belgian Institute of Natural Sciences, Bruxelles, Belgium

³Bristol Zoological Society, c/o Bristol Zoo Gardens, Clifton, Bristol, UK

⁴Malagasy Veterinary Consultant, Antananarivo, Madagascar

Correspondence

Leslie Wilmet, TERRA Research Center, Forest is Life, Gembloux Agro-Bio Tech, University of Liège. Passage des Déportés, 2. B.5030 – Gembloux Or 73, rue Wayenberg, 1050 Bruxelles. Belgium.
Email: leslie.wilmet@hotmail.com

Funding information

Mohamed Bin Zayed Fund; AEECL; Nature +; Liège University - Gembloux Agro-Bio Tech; Rufford Foundation; FNRS-FRIA; Fondation Leopold III

Abstract

Lepilemur mittermeieri, a little-studied sportive lemur of north-west Madagascar, endemic to the Ampasindava Peninsula, faces habitat loss through forest degradation and rapid fragmentation. Understanding its habitat requirement is the first step toward preservation of this threatened forest-dependent species. In this study, we gathered data on the use of space and home range characteristics of *L. mittermeieri*. We studied individuals from early March to the end of June 2015 and 2016, in three sites of the Ampasindava peninsula. We radio-tracked 15 individuals to obtain detailed information on the size and location of home ranges (around 450 hr of tracking). Direct observation and morphometric measurements provided additional data sets. Both kernel density estimation (KDE) and minimum convex polygon (MCP) methods yielded similar home range sizes (an average of 2.01 ha with KDE method and 1.96 ha with MCP method). We did not find differences in home range size between males and females, with respect to forest type or proximity to the forest edge. Home ranges overlapped and individuals showed low levels of territoriality. We highlighted a sexually-dimorphic trait: males have longer upper canine than females. Our results constitute the first set of ecological information on *Lepilemur mittermeieri* and could be the basis for a conservation strategy for this endangered species with a very small distribution area.

KEYWORDS

conservation, habitat use, *Lepilemuridae*, radio-tracking

1 | INTRODUCTION

Lepilemur mittermeieri is an endangered forest-dwelling lemur, endemic to the Ampasindava peninsula in north-west Madagascar (IUCN, 2012; Mittermeier et al., 2010). It was described in 2006 on the basis of genetic material (Rabarivola et al., 2006). Very little was known on its ecology and precise distribution prior to 2014. The species has now been observed in several patches of two forest types of the Ampasindava peninsula (Wilmet, Schwitzer et al., 2017): dense humid forests and older secondary forests. These habitats are

severely impacted by degradation and fragmentation, under the increasing pressure of human population growth, agricultural extension, logging and exploitation of natural resources (MBG, 2015; Tahinarivony, Rasoanaivo, Ranirison, Rasolofo, & Gautier, 2015; Tahinarivony et al., 2017; Wilmet, Devillers, & Beudels-Jamar, 2017), which raises serious concerns about the future of *L. mittermeieri*. Relatively little is known, however, about its habitat requirements. No quantitative data on important ecological traits such as home range size, territoriality, or edge avoidance exist. This contribution aims to provide the first set of preliminary data on these

eco-ethological traits, the understanding of which is essential to define conservation measures.

Home range size is a key parameter in the evaluation of a species spatial needs (Schwitzer, Glatt, Nekaris, & Ganzhorn, 2011; Seiler, Holderied, & Schwitzer, 2015). Ranging behavior is particularly relevant in the context of a fragmented and degraded habitat where forest patches may vary in quality and abundance of resources (Gabriel, 2013). A functional definition of the home range of an animal is proposed by Burt (1943): “[The] home range [is] that area traversed by the individual in its normal activities of food gathering, mating and caring for young. Occasional sallies outside the area, perhaps exploratory in nature, should not be considered as in part of the home range.” Other important questions include how space is partitioned, that is, the ability of individuals to share part of their home range with others (Mcloughlin, Ferguson, & Messier, 2000), and whether animals display territorial behavior and actively defend their home range—or part of their home range—against conspecifics (Begon, Harper, & Townsend, 1986).

When continuous monitoring is possible, the home range is calculated by the envelope of points of frequent presence. However, in many cases monitoring is discontinuous and a statistical approach is necessary to estimate the home range. Several methods have been devised (e.g., grid-cell method, minimum convex polygon (MCP), kernel density estimation (KDE), local convex hull), based on the distribution and density of the contacts obtained, without taking into account the reasons underlying the use of space by the animal, nor its variation through time (Powell & Mitchell, 2012).

Habitat fragmentation processes increase the extent of edge areas, which may have a positive or negative influence on forest-dwelling species (Quéméré et al., 2010). Indeed, species respond in diverse ways to the proximity of edges (Anderson, Rowcliffe, & Cowlshaw, 2007; Lehman, Rajaonson, & Day, 2006; Quéméré et al., 2010). Edge effects are usually defined as the penetration, to varying depths and intensities, of conditions from the surrounding environment into the forest interior (Lehman et al., 2006; Malcolm, 1994).

In this study, we (a) evaluate the mean size of the nocturnal home range of *Lepilemur mittermeieri*, using two methods, MCP and KDE, (b) investigate home range size variation between male and female and between two forests types (dense humid forests and older secondary forests), (c) investigate home range location with respect to edge areas, and (d) evaluate territoriality. On the assumption that the size and characteristics of the home range of *L. mittermeieri* are similar to those of six other sportive lemurs studied so far (Ganzhorn et al., 2004; Hilgartner, 2006; Hladik, Charles-Dominique, Martin, Doyle, & Walker, 1974; Zinner, Hilgartner, Kappeler, Pietsch, & Ganzhorn, 2003; Dinsmore et al., 2016; Mandl, 2018; Rasoloharijaona, Randrianambinina, Braune, & Zimmermann, 2006; Seiler et al., 2015), we expect *L. mittermeieri* to have home ranges of around 1 ha, males and females to have similar home range sizes (Mandl, 2018; Seiler et al., 2015; Zinner et al., 2003), and home ranges to be located randomly in the forest or near forest edges (Lehman et al., 2006; Lehman, 2007; Mandl, 2018; Wilmet, Schwitzer et al., 2017). We also expect home ranges to be nonexclusive, as home range

overlap was observed for other *Lepilemur* species (Hilgartner, 2006; Droscher & Kappeler, 2013; Mandl, 2018).

2 | MATERIAL AND METHODS

2.1 | Study area and sites

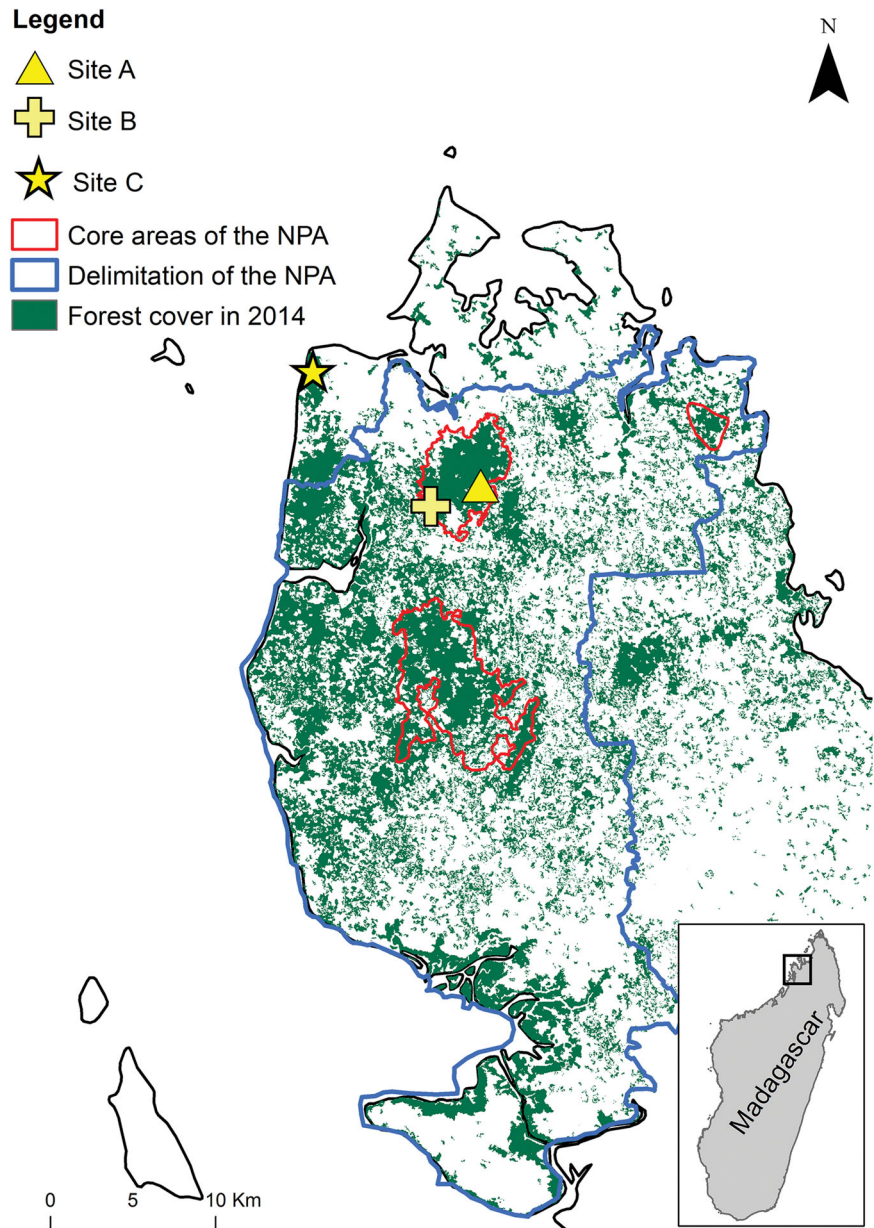
We worked on the Ampasindava Peninsula, located along the coast of the Mozambique Channel, between 13°30' and 13°58' latitude south and 47°42' and 48°42' longitude east, in north-western Madagascar (Figure 1). Part of the peninsula was designated as a “new protected area” in 2015. Three core areas, mostly forested, covering some 7,648 ha, have been identified (Figure 1; MBG, 2015). Altitudes range from 0 to 720 m a.s.l. with a rough, hilly terrain. The peninsula is characterized by a hot, humid/subhumid climate and is part of the Sambirano Domain (*sensu* Humbert, 1951). Two main forest types are widespread on the Ampasindava Peninsula, dense humid forests, with low perturbation levels, and older secondary forests (Tahinarivony et al., 2017). We selected three study sites, ensuring a wide representation of landscapes and forest types. The first two sites, site A and site B, are situated on the slopes of Mount Andranomatavy in a remaining large patch of dense humid forest with low perturbation (2,534 ha; MBG, 2015; Rasoanaivo & Tahinarivony, 2015). They are located inland (Figure 1). Data were gathered at elevations between 170 and 435 m a.s.l. Mount Andranomatavy is within the core area of the protected area, which limits anthropogenic disturbance. Site C is covered with older secondary forests and is located along the north-west coast of the Peninsula (Figure 1). This site is an isolated forest patch of 167 ha at a maximum elevation of 200 m a.s.l. and is surrounded by clearings (Wilmet, Schwitzer et al., 2017). As site C is located outside the protected area (Figure 1), the level of anthropogenic disturbance is higher than in the other two sites, mainly due to illegal logging. In site C we observed large quantities of bamboo (*Nastus* sp.), an indicator of former selective logging (Seiler, 2012).

2.2 | Study subject

2.2.1 | Capture method and handling procedures

We located *Lepilemurs* at night by eyeshine or vocalization. They were caught by remote immobilization, using a CO₂ powered dart rifle (DanInject JM rifle) in combination with 0.5 cc volume darts (Pneu-Dart P-type projectiles) or blowpipe (Pneu-dart blo-jector kit) in combination with 1.5 blowpipe syringes. Darts were loaded either with tiletamine/zolazepam (Telazol®, Fort Dodge Animal Health, 15 mg/kg) or a combination of ketamine and xylazine (K10mg/kg + X0.2 mg/kg; Lei et al., 2008). We recorded morphometric measurements, examined anesthetized individuals medically and then equipped them with radio-collars. We released individuals at their exact capture location. After nearly 3 months of monitoring, we caught the individuals again, weighed them and removed their radio collar.

FIGURE 1 Map of the Ampasindava peninsula located in north-west Madagascar, with the forest cover of 2014. The three study sites, the new protected area (NPA) delimitation and its three core areas are represented



2.2.2 | Studied individuals

In total, as part of two field missions, we captured 21 *Lepilemur mittermeieri*. As animals cannot be sexed prior to capture, it was not possible to secure a sexually balanced sample. We caught as twice more males than females but we do not have an explanation for this sex bias. In 2015, five individuals were caught in the inland site A (all males) and five individuals in the coastal site C (three males and two females). In 2016, we caught five individuals in the inland site B (four males and one female) and six in the coastal site C (two males and four females) where none of the individuals from 2016 were recaptured. Biometric data were collected for all 21. Through radio-tracking (Biotrack-Dorset-UK PIP3 Tag-cable tie collar. Weight < 4.5 gr.), we were able to obtain location with respect to edge areas data for 16 of them and activity data for 15 of them (four males in site A, four males in site B and in four females and three

males in site C). For 6 of the 21, radio-tracking data were not obtained. One of them died during capture operation, two were fitted with collars but chewed their collar off before release and three were released with collars but signal contact was lost rapidly. This loss of contact may have resulted from predation, damage to the collar or movement of the animal out of the range of the detector.

2.3 | Home range and behavior monitoring

We collected data on the home range during six months (two missions conducted in 2015 and in 2016), from the beginning of April to the end of June. This period coincides with the end of the rainy season and the beginning of the dry season. The geographically close *Lepilemur sahamalaza* is most active during this period (April to June), which corresponds to its mating season (Mandl, 2018; Seiler et al., 2015).

It was thus a reasonable assumption that this would also be a favorable time for monitoring the activity of *L. mittermeieri*. For radio-tracking techniques we followed common practice in the determination of the home range of small nocturnal primates, such as nocturnal lemurs, bushbabies and lorises (Wiens, 2002; Nekaris, 2003; Dinsmore et al., 2016; Pimley, Bearder, & Dixon, 2005; Seiler et al., 2015.). We followed the 15 radio-collared individuals using a Sika receiver-8 MHz and a Lintec flexible 3-element Yagi antenna to follow each individual for six hours per night, from 6 p.m. to 12 p.m. We recorded GPS points every 10 minutes (Garmin 62S) from first visual contact with the animal. Total tracking time for each of the 15 individuals in the three study sites (A, B, and C) varied according to field conditions (first visual contact, rain, receptor problems), with a minimum of 22 hours and 45 minutes (five half nights) and a maximum of 34 hours and 44 minutes (seven half nights; Table 1). As individuals continued to be active when observed (for example feeding) and never tried to flee in our presence, we are confident that the presence of observers did not significantly disturb the animals.

While gathering data on the focal individuals, we sighted other sportive lemurs (by direct observation or by vocalizations) within the home range of the tracked individuals. We also collected information on basic social interactions between sportive lemurs using direct observation and the focal sampling method (Altmann, 1974) on individuals equipped with radio-collars.

TABLE 1 Nocturnal home range size calculated through kernel density estimation and minimum convex polygon methods for the 15 individuals studied

Site	Sex	Code of the animal	Hours of GPS recording	NHR size (ha) Kernel 50%	NHR size (ha) Kernel 95%	NHR size (ha) MCP
Site A & Site B (Inland sites)	M	D1501	22H58	0.92	4.81	5.68
	M	D1503	22H45	0.18	0.77	0.40
	M	D1505	26H19	0.66	2.93	2.97
	M	D1506	34H44	0.54	2.97	2.96
	M	D1601	33H42	0.23	1.04	0.82
	M	D1603	28H43	0.36	1.53	1.60
	M	D1604	33H43	0.71	2.86	2.75
	M	D1605	31H50	0.47	1.91	1.99
Site C (Coastal site)	M	S1501	28H11	0.27	1.15	1.49
	M	S1502	25H39	0.52	2.19	1.74
	F	S1503	26H36	0.46	1.96	1.75
	F	S1504	29H39	0.41	1.64	1.49
	F	S1604	33H05	0.39	1.80	1.54
	M	S1605	35H33	0.30	1.65	1.47
F	S1606	33H28	0.23	0.97	0.72	

Note: Summary of information related to each individual: site, sex (M = male or F = female), animal code and hours of GPS recording. Abbreviations: KDE, kernel density estimation; MCP, minimum convex polygon; NHR, nocturnal home range.

2.4 | Data analysis

2.4.1 | Home range size evaluation and comparison

Generally, home range studies consider study sites as if they were totally flat (Monterroso, Sillero, Rosalino, Loureiro, & Alves, 2013). As our study sites were located on slopes, we investigated a possible influence of the third dimension in the evaluation of the home-range size. The mean slopes calculated for each of the sites were below or close to the 16.3° value under which Monterosso et al. (2013) found no significant error ($\leq 5\%$) in ignoring the declivity.

We used two classical approximations to evaluate the home ranges of tracked individuals. The MCP consists of the calculation of the smallest convex polygon enclosing all the relocations of the individual (Hayne, 1949). The KDE method (Seaman & Powell, 1996; Silverman, 1986) estimates a bivariate probability density function (UD; Worton, 1989). The number of sample points we gathered per individual, 111 to 375 (average 210), is amply sufficient for the application of the KDE method (Seaman et al., 1999). The smoothing parameter “*h*” controls the “width” of the kernel functions placed over each point. One of the most common choices for this parameter is the so-called “reference bandwidth.” As a large variation of the “reference bandwidth” exists among our samples, we used a uniform smoothing parameter ($h = 13.98$), corresponding to the average “reference bandwidth” value of all individuals. Nocturnal home ranges were defined as the minimum area in which there is a 95% probability to find the animal (Calenge, 2015; Worton, 1989). The core area of the home range is defined as the minimum area in which there is a 50% probability of encounter (Calenge, 2015; Worton, 1989). We generated the unimodal symmetrical bivariate probability density function through the AdehabitatHR package in R. We then used ArcGIS10.1 to map the results. We used the R environment to perform the statistical nonparametric Mann-Whitney U test to compare home ranges of males and females at the coastal site (site C) and to compare the home ranges of males in two forest types (dense humid forests with low perturbation, sites A and B, and older secondary forests, site C).

2.4.2 | Home range overlapping and basic social interaction

The mapping of the nocturnal home range allowed visual identification of home range overlaps between individuals. To identify potential territorial behavior, we counted the occurrence of different types of behavior (no reaction, agonistic behavior, escape, pursuit, vocalization).

2.4.3 | Mean distance traveled

We measured the mean distance traveled by individuals over a half-night (from 6 p.m. to midnight) using the Garmin Basecamp (version 4.1.2) software. We corrected the distance observed each night by a factor that takes into account the duration of the tracking for that night. We assumed that animals moved in a straight line

between the points recorded at 10-min intervals (Serena, 1984) which may underestimate the actual distance traveled (Sennhenn-Reulen, Diedhiou, Klapproth, & Zinner, 2017). We used the R environment to perform the Spearman correlation test to evaluate if a correlation existed between the mean distance traveled and the home range size.

2.4.4 | Home range location with respect to edge areas

To investigate the possibility of a relation between home range and location with respect to forest edges, we used the 2014 forest cover maps produced by CIRAD (Vieilledent et al., 2018) and selected the Ampasindava peninsula area using ArcGIS10.1. In the first approximation, we arbitrarily designated as “edge area”, a 170 m wide strip around the forest patches. This 170 m width was chosen because it represents the distance from the edge to which its effects were found to prevail in a study of the gradients of diverse environmental parameters conducted in nearby Sahamalaza peninsula by Mandl (2018). We then determined whether the nocturnal home range of individuals was located (or mostly located) within this edge area, or was entirely (or mostly) contained within the core area of the forest. We used the R environment to perform the statistical nonparametric Mann–Whitney U test to compare nocturnal home range sizes of individuals living predominantly within the edge area to that of individuals living predominantly within the core area.

2.5 | Ethical note

This research received all research permits required and complies with the protocols approved by the Missouri Botanical Garden who manages the area and adheres to the legal requirement of Madagascar's Association Nationale pour la Gestion des Aires Protégées. The study was conducted in compliance with the American Society of Primatologists' Principles for the Ethical Treatment of Primates. The authors declare no conflict of interest.

3 | RESULTS

3.1 | Morphometric

In April 2015 and 2016 we collected morphometric data from 6 adult females, 1 juvenile female, 13 adult males, and 1 juvenile male. Among *L. mittermeieri* adults only, we calculated an average body mass of 705 ± 46.27 g without variation between males and females ($N = 19$, Mann–Whitney U test: $W = 43.5$, $p = .725$). We measured a head-body length of 25.5 to 30.3 cm, and a tail length of 22.6 to 28.1 cm (Table 2). We observed sexual dimorphism in the size of upper canines: males have, on average, longer upper canines (5.2 ± 0.65 mm) than females (3.94 ± 0.94 mm) ($N = 19$, Mann–Whitney U test: $W = 5$, $p = .002$).

TABLE 2 Body size and canine length of adult males and females *L. mittermeieri*

Body part	Sex	Mean	N	SD	Range
Body mass (g)	f	710	6	48.17	640 - 760
	m	702.69	13	47.19	630 - 810
Head-body length (cm)	f	27.78	6	1.67	25.5–30.1
	m	28.55	13	1.25	26.7–30.3
Tail (cm)	f	25.02	6	1.87	22.6–27.1
	m	25.8	13	1.12	24.2–28.1
Femur (cm) *	f	8.73	6	1.28	6.2–9.7
	m	9.97	13	0.86	8.5–11.3
Tibia (cm)	f	8.92	6	1.13	7.9–10.4
	m	9.37	12	1.47	7.7–11.2
Foot (cm)	f	7.18	6	0.78	6–8.2
	m	7.79	13	0.5	7–8.7
Upper arm (cm)	f	5.78	6	0.35	5.4–6.4
	m	6.07	12	0.6	5.1–7
Forearm (cm)	f	6.15	6	0.42	6–7.2
	m	6.96	13	0.81	6.3–8.8
Hand (cm)	f	5.08	6	0.12	4.9–5.3
	m	5.18	13	0.37	4.6–5.5
Upper canine (cm) *	f	4.01	6	0.16	3.1–4.8
	m	5.20	12	0.64	3.8–5.8
Lower canine (mm)	f	3.43	6	0.38	2.81–3.7
	m	3.38	13	0.59	2.07–3.9

Note: Measurements of body parts that differ significantly between males (m) and females (f) are marked with an asterisk. (Data from March 2015 and 2016).

Abbreviation: SD, standard deviation.

3.2 | Home range size evaluation and comparison

Nocturnal home range sizes calculated through the two methods (MCP and KDE) are presented in Table 1. The mean home range size of the 15 marked *Lepilemur* is $2.01 \pm$ standard deviation (SD) 1.04 ha using the KDE method 95%. A similar result, $1.96 \pm$ SD 1.28 ha, is obtained using the MCP method.

Comparison of home range sizes (using KDE method) between males and females (from site C) shows no significant difference ($N = 7$, Mann–Whitney U test: $W = 6.5$, $p = 1.0$). Home range sizes of males in the two forest types (dense humid forests of sites A & B and older secondary forests of site C) show no significant difference ($N = 11$, Mann–Whitney U test: $W = 15$, $p = .630$).

3.3 | Home range overlap, basic social interaction, and mean distance traveled

Figures 2–4 shows the home ranges of all marked individuals. Clear overlaps appear for four males in site A and site B (D1501–D1503 and D1601–D1604; Figures 2,3). No overlap is observed between marked individuals at site C, but this may be due to the distance

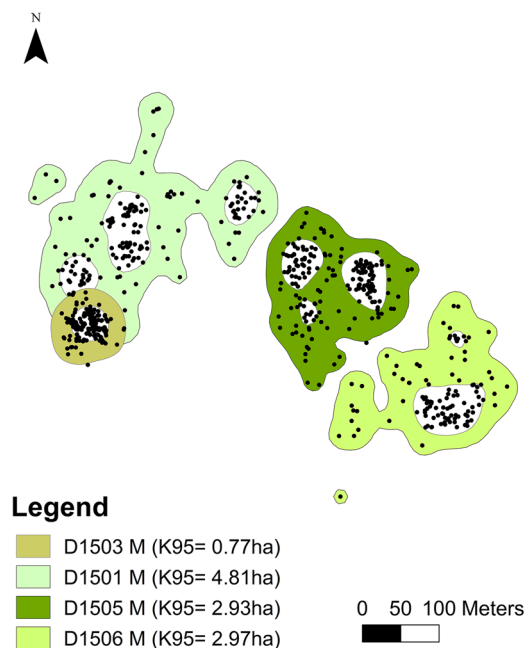


FIGURE 2 Map of the home range of the four males studied in site A. Kernel at 95% is represented by a colored area, kernel at 50% by the white interior area. The surface of the kernel at 95% (K95) is provided in hectares. Dots are the GPS records at 10-min intervals

between these individuals (Figure 4). We spotted unmarked individuals within the range of the marked individuals every night during the whole survey period (from 1–4 contacts per nights, which may include some double contacts of the same individual). Relatively few territorial reactions were observed between animals. During the 450 hr of total tracking time, only 51 territorial interactions were

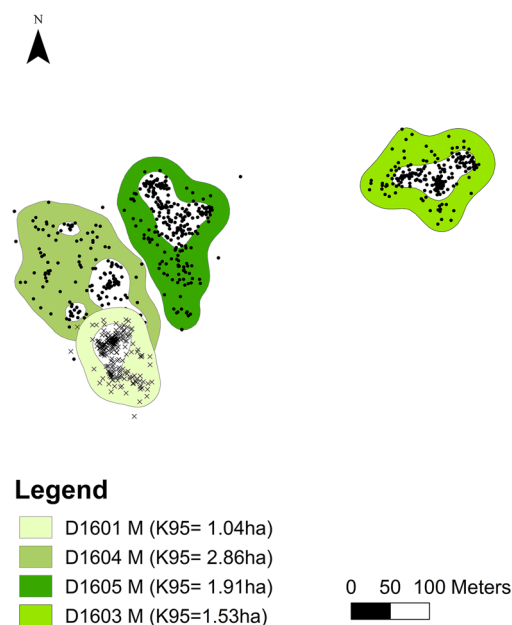


FIGURE 3 Map of the home range of the four males studied in site B. Kernel at 95% is represented by a colored area, kernel at 50% by the white interior area. The surface of the kernel at 95% (K95) is provided in hectares. Dots are the GPS records at 10-min intervals

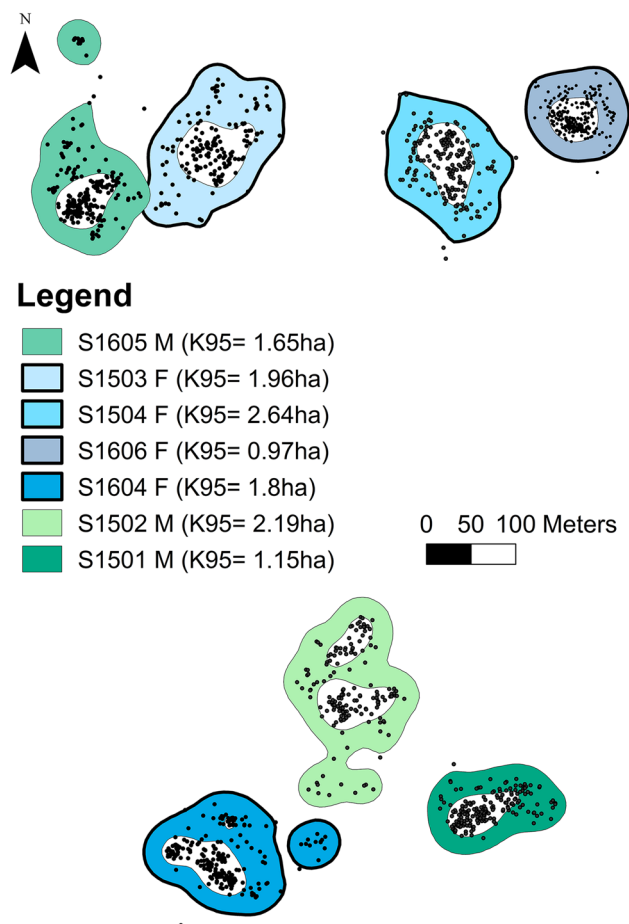


FIGURE 4 Map of the home range of the seven individuals studied in site C. Kernel at 95% is represented by a colored area, kernel at 50% by the white interior area. The surface of the kernel at 95% (K95) is provided in hectares. Dots are the GPS records at 10-min intervals. Shades of green denote the home ranges of males (M), shades of blue those of females (F), which also have a thicker contour line. The separation between individuals was verified along two transect lines

observed (Table 3). The absence of reaction in the close presence of another individual was the norm (19 observations). We identified few agonistic behaviors (four observations). In many cases, individuals distanced themselves from others by jumping a few meters away (11 observations). In some cases, individuals jumped and followed each other into the forest, one pursuing the other (10 observations). We also observed animals vocalizing as a direct reaction to the approach of another individual (7 observations).

The mean travel distance per half-night is 570.3 ± 145.5 m. There is a significant correlation between mean distances traveled and nocturnal home range sizes (Spearman correlation test: $r_s = 0.61$, $p = .015$; Figure 5): individuals with larger home ranges travel longer distances.

3.4 | Home range location with respect to edge areas

In each study site, some home ranges were located within edge areas (Figures 6,7). No significant difference in home range size was

TABLE 3 Territorial behaviors observed during the 450 hr of tracking among all marked individuals. Five types of behavior were recorded

Number of observation	Type of behavior	Description of the behavior
19	No reaction	No movement/ no direct reaction from the animal/ the animal does not change its activity
4	Agonistic behavior	Two animals are observed having brief seemingly threatening contact/they face each other instead of escaping/ a lot of noise may be made in the trees/sometimes one animal falls.
11	Escape	One animal jumps away within 5 meters in the presence of another animal and is not followed.
10	Pursuit	One animal is chased by another.
7	Vocalization	One animal vocalizes in direct/obvious reaction to another.

found between the 10 animals located in the edge area and the 5 individuals living in the forest core area ($N = 15$, Mann-Whitney U test: $W = 25$, $p = .864$).

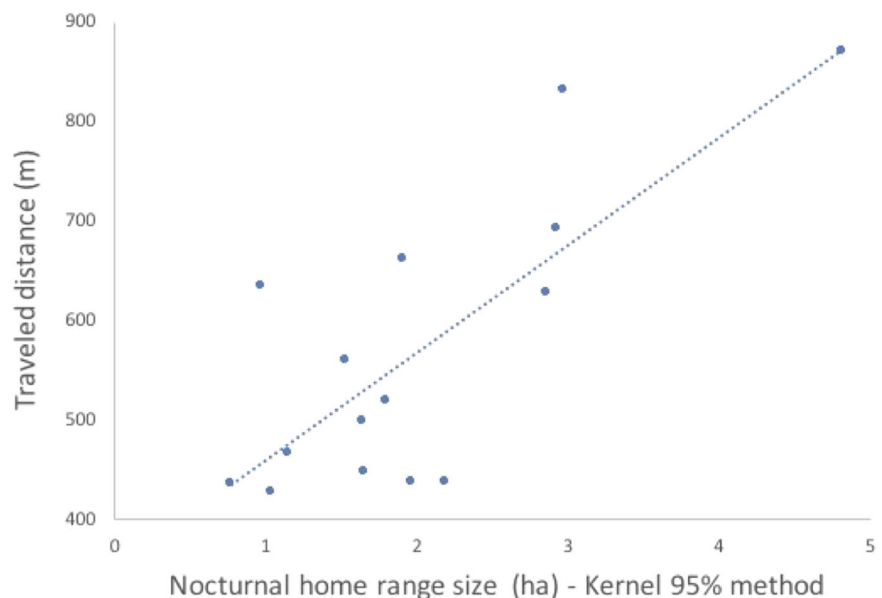
4 | DISCUSSION AND CONCLUSION

This research presents the first large data set (21 individuals) on the morphometrics of *Lepilemur mittermeieri*. Our measurements of head-body and tail length show a greater spread than the data currently available for the species (Mittermeier et al., 2010). The average body size calculated, 705 g, is close to the 730 g given by E. E. Louis Jr. (Mittermeier et al., 2010). Our data show no weight difference between males and females, a result also obtained for *L. ruficaudatus* (Zinner et al., 2003). In other species, *L. mustelinus* for example, females are heavier than males (Rasoloharijaona, Randrianambinina, & Zimmermann, 2007) while in *L. sahamaza* females seem to be lighter than males (Mandl, 2018). Our observation of sexual dimorphism in canine size suggests that males *L. mittermeieri* compete for important resources, such as access to females, a hypothesis also formulated for *L. ruficaudatus* by Zinner et al. (2003). *Lepilemur* is known to be cryptic species (Schwitzer, Mittermeier, Louis, & Richardson, 2013), and we confirm that visual observation cannot be used to differentiate *L. mittermeieri* from *L.*

sahamalaza, *L. dorsalis*, *L. tymerlachsonorum*, or *L. ankaranensis* and probably others.

Our preliminary results suggest that *Lepilemur mittermeieri* has nonexclusive home ranges of around 2 ha (KDE and MCP method). More data are needed to determine if *L. mittermeieri* modifies its home range size and location according to seasons. Even if the comparison of home range sizes between species needs to be taken with caution as methods differ (Laver & Kelly, 2008), orders of magnitude can be discussed. The mean home range we observed is very similar to that found for *Lepilemur septentrionalis* (1.96 ha; Dinsmore et al., 2016). *L. septentrionalis* and *L. mittermeieri* appear to have larger home ranges than the other *Lepilemur* studied so far. The average home range of *Lepilemur mustelinus* is estimated at 1.5 ha (Ratsirarson & Rumpler, 1988). Three other species, *L. ruficaudatus*, *L. edwardsi*, and *L. leucopus*, have home range sizes of around 1 ha (Ganzhorn et al., 2004; Hilgartner, 2006; Hladik et al., 1974; Rasoloharijaona et al., 2006). *L. sahamalaza* may have an even smaller home range: Seiler et al. (2015) estimated the mean size at 0.38 ha, but a recent study indicated a larger size of 0.67 ha (Mandl, 2018).

Folivorous *Lepilemur* has rather small home ranges compared with other small nocturnal species with different diets. For example, a mainly frugivorous mouse lemur (Lahann, 2008), *Microcebus murinus* (81 g), has a mean home range of 0.7 to 1.6 ha for females and 2.8 to 4.8 ha for males (Lahann, 2008). Another small nocturnal primate (100–180 g),

**FIGURE 5** Traveled distance versus nocturnal home range size for each individual

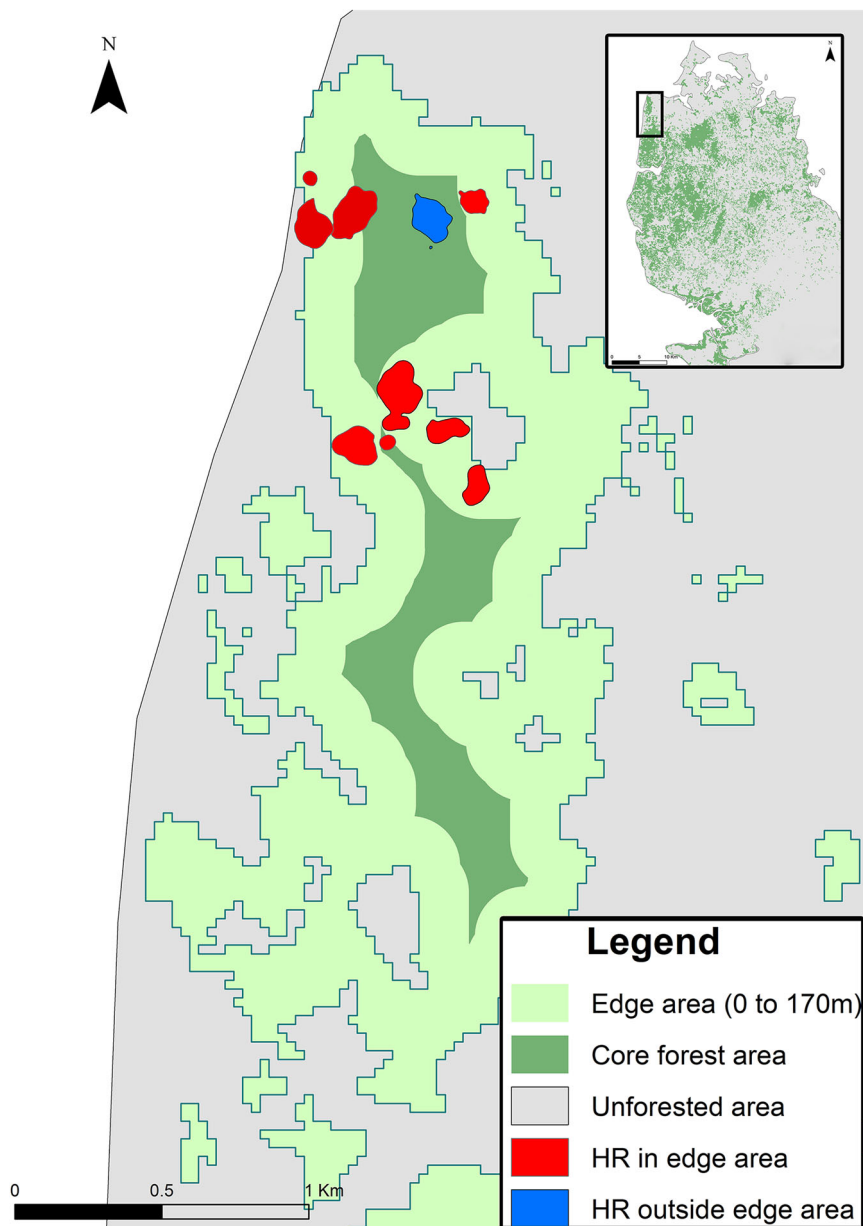


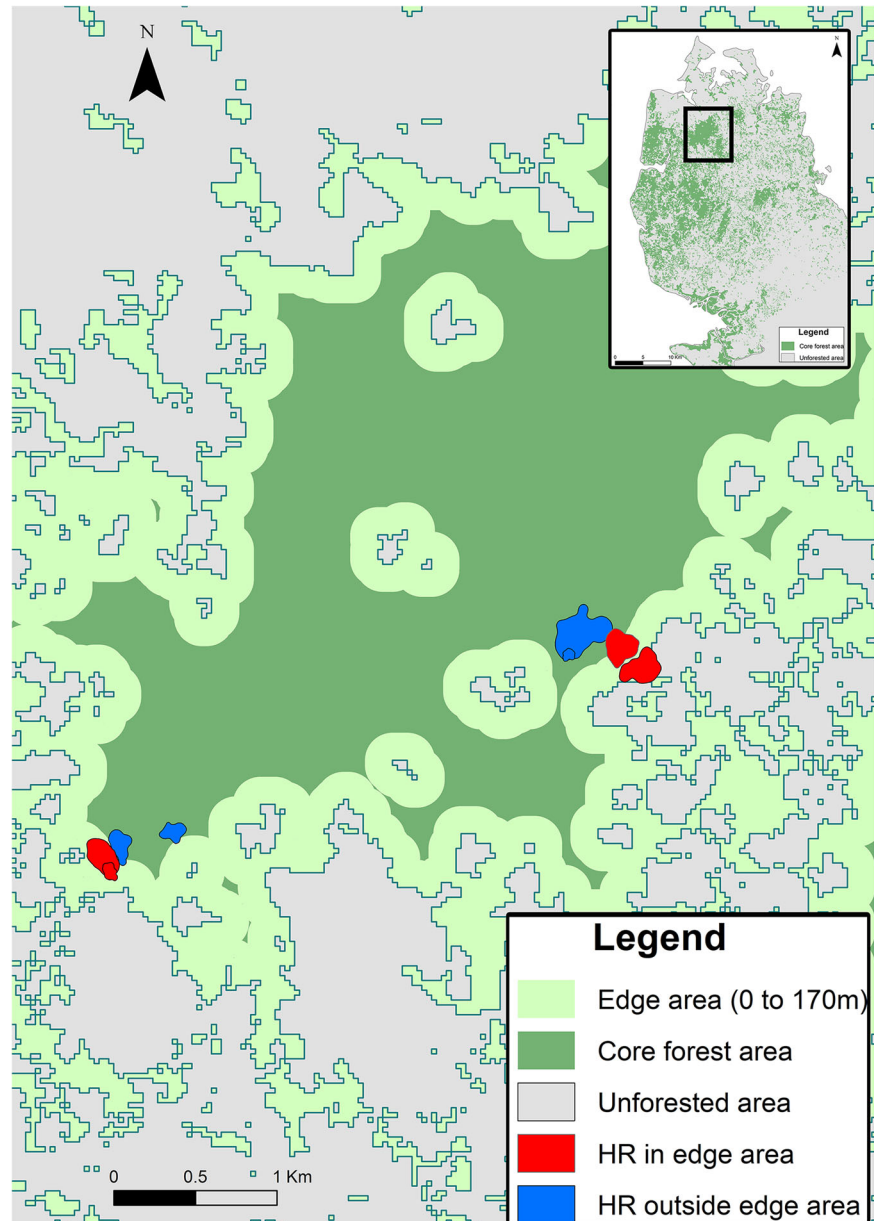
FIGURE 6 Map of the home range (HR) location with respect to edge areas of the eight individuals studied in site C

Loris tardigradus tardigradus, that is mainly insectivorous, has an average home range of 2.6 ha for males and 3.7 ha for females (Nekaris, Stengel, Marsh, & Chapman, 2013). This may be related to a “energy minimizing” strategy for folivorous (Kay, Covert, Chivers, Wood, & Bilsborough, 1984). Indeed, it has been shown that *L. leucopus* possess the lowest mass-specific metabolic rates measured so far for an endotherm (Bethge, Wist, Stalenberg, & Dausmann, 2017) and *L. ruficaudatus* has a reduced metabolic rate during its resting periods (Ganzhorn, 2002; Schmid & Ganzhorn, 1996; Seiler et al., 2015). *L. sahamalazensis* and *L. leucopus* rest often during the night (Nash, 1998; Seiler, 2012), a strategy we observed also in *L. mittermeieri*. However, it is not necessarily true that the size of the home range is a reliable measure of energy expenditure, as this is more related to activity patterns and the distance traveled within the range.

Home ranges of *Lepilemur mittermeieri* were not exclusive to individuals and no obvious pattern of territorial defense was observed. This is similar to what Mandl (2018) found for *L. sahamalaza*. The absence of significant differences between the home ranges of males and females, corresponds to the general observation made for most *Lepilemur* studied so far, that is, *L. ruficaudatus*, *L. sahamalaza*, *L. edwardsi*, *L. mustelinus* (Hilgartner, 2006; Mandl, 2018; Seiler et al., 2015; Zinner et al., 2003). In *L. leucopus*, on the contrary, males have larger home ranges than females (Droscher & Kappeler, 2013), which has also been reported for other small nocturnal primates, such as *Loris lydekkerianus lydekkerianus* (Nekaris, 2003) and *Microcebus murinus* (Lahann, 2008).

The two habitat types investigated, “dense humid forest with low perturbation” and “older secondary forest,” seem equally suitable for

FIGURE 7 Map of the home range (HR) location with respect to edge areas of the four individuals studied in site A (on the right) and the four individuals studied site B (on the left)



L. mittermeieri, as no significant home range size variation was found. The finding that sufficient resources thus seem to be found in both forest types is of high importance for the conservation of the species, as the forest habitats of the Ampasindava peninsula are highly threatened (Tahinarivony et al., 2017). The correlation we find between range size and distance traveled by individuals suggests, however, that resources are less concentrated in the larger home ranges, which may correspond to forest heterogeneity within the two habitat types investigated. The distance traveled during half nights by *L. mittermeieri* (570 m) is longer than that observed for *Lepilemur edwardsi* (343 m for all night) and *L. leucopus* (270 m for all night; Schwitzer et al., 2013). This may be related to differences in forest composition.

L. mittermeieri does not avoid edge areas. The same tolerance has been observed for three other sportive lemurs, *L. microdon*, *L. mustelinus*, and *L. sahamalaza* (Lehman et al., 2006; Lehman, 2007; Mandl, 2018). This tolerance is typical of folivorous species (e.g. *Propithecus tattersalli*),

which usually do not display clear edge effects (Quéméré et al., 2010). Primates with different diets show different patterns. Preference for forest edges has been observed for a number of insectivorous primates (e.g., *Micorcesus rufus*, *Micocebus ravelobensis*, *Tarsius pumilus*, *Loris tardigradus tardigradus*; Bernede, Bearder, & Gunawardene, 2012; Lehman et al., 2006; Burke & Lehman, 2014; Grow, Gursky, & Duma, 2013), and edge avoidance has been observed for some frugivorous primates (e.g for *Propithecus coquereli* (Kun-Rodrigues et al., 2014) or *Eulemur fulvus rufus* (Lehman et al., 2006)).

The forest cover of the Ampasindava is highly fragmented and under high pressure of deforestation (Tahinarivony et al., 2017). Presence of *L. mittermeieri* in edge areas is thus of high importance for the development of conservation strategies. Indeed, if only core forest areas were suitable for the species, the effective surface available for *L. mittermeieri* would be very small or non-existent in many forest patches. It appears on the contrary that *L. mittermeieri*

finds sufficient resources in edge areas, as the size distribution of home ranges of individuals living within these edge areas is similar to that of individuals living within core areas.

Our study provides information on the spatial requirements of the endangered *Lepilemur mittermeieri* and, more generally, contributes to the understanding of the space needs of small nocturnal primates. It is a first step in answering a larger question: how deforestation and habitat fragmentation affects *L. mittermeieri*. The ability of this species to live in edge areas is an important result in the context of fragmentation. Nevertheless, the species remains threatened by current and future forest degradation throughout the peninsula. The impact of this anthropogenic process on *Lepilemur mittermeieri* should be investigated throughout the Ampasindava peninsula. Several forest fragments of varied sizes and types still harbor the species, and further analysis is needed to evaluate the long-term survival prospect of the species in these fragments. The current management plan of the protected area identifies three core areas (Figure 1) in which conservation efforts should be particularly intense. Our results show that coastal forests also seem to meet the needs of *L. mittermeieri*, at least in their current state. If the protection of large forest patches is a first priority, preventing further forest degradation in the smaller coastal fragments is also crucial and should not be forgotten in conservation strategies. In addition, efforts should be made to maintain and/or restore connectivity between several forest fragments. These measures cannot be implemented successfully without a reduction of anthropogenic pressure achieved by the development, in consultation with local communities, of viable alternatives to the present use of forests.

ACKNOWLEDGMENT

We are grateful to the Ministère de l'Environnement et des Eaux et Forêts de Madagascar for allowing us to carry out research in the new protected area of the Ampasindava peninsula. We are thankful to professors from the Département de Paléontologie et d'Anthropologie Biologique de la Faculté des Sciences (Department of Paleontology and Biological Anthropology) of the Antananarivo University for their collaboration and for the field assistance of Tahiriaina Randriarimanga (Tahiry) and Simon Razafindramoana. We thank the Managed Resources of Protected Area (MRPA) and the Missouri Botanical Garden and in particular Prof. Patrick Ranirison and Dr. Brice Funk Lee Rakotorasafy for their help and precious advice. We thank the Madagascar Biodiversity Partnership for the capture of *lepilemur* and collar placement in April 2015. We thank our research field assistants; DD, Antony, and Mila, as well as Loïc & Valérie (Naturalia Lodge), for their great support during each mission. The field missions were possible thanks to seven grants and funding from the Foundation Leopold III, AEECL, Nature+, Rufford Foundation, Mohamed Bin Zayed Fund, FNRS-FRIA, and Liège University - Gembloux Agro-Bio Tech. We also would like to thank Prof. Adeline Fayolle, Prof. Philippe

Lejeune, Prof. Yves Brostaux, and Dr. Fany Brotcorne from Liège University, Gembloux Agro-Bio Tech for their precious advice and help for the analysis of the data. The authors wish to thank Jean Devillers-Terschuren for the revision of the manuscript.

ORCID

Leslie Wilmet  <http://orcid.org/0000-0002-9007-7786>

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How to cite this article: Wilmet L, Beudels-Jamar RC, Schwitzer C, Rakotondrainibe H, Devillers P, Vermeulen C. Use of space and home range characteristics of *Lepilemur mittermeieri*, an endangered sportive lemur endemic to the Ampasindava peninsula, north-west Madagascar. *Am J Primatol*. 2019;e23017. <https://doi.org/10.1002/ajp.23017>