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Updated population density estimation and distribution range of the Critically Endangered Sahamalaza sportive lemur, *Lepilemur sahamalaza*

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Abstract
Accurate population density estimates are important for effective conservation measures of endangered species. For the Critically Endangered Sahalamaza sportive lemur (*Lepilemur sahamalaza*), no recent or robust population estimates are available, complicating conservation management of this species. This study examined the species distribution range as well as assessing population density in the range of occurrence with standardized methodology (transect walks and home range calculations) between 2013 and 2016. The results suggest that Sahamalaza sportive lemurs are confined to the Sahamalaza Peninsula. Population density ranges between 1.49 to 1.87 individuals/ha depending on the methodology used to estimate density. Population size estimates consequently vary between 3800 and 4700 remaining individuals of this species, subject to a re-evaluation of the remaining habitat.

Introduction
The nocturnal and arboreal Sahamalaza sportive lemur (*Lepilemur sahamalaza*) (the name was changed recently from *L. sahamalazensis*, Andriaholinirina *et al.,* 2017), remains comparatively unstudied despite facing pressing conservation issues, the most prominent issue being loss of habitat from anthropogenic pressure (Schwitzer *et al.,* 2006; Seiler *et al.,* 2010, 2013a; Volampeno *et al.*, 2013). This species occurs only in the northwest of Madagascar and is believed to be confined to the forests on the Sahamalaza Peninsula which was proclaimed a National Park in 2007 (Schwitzer *et al.*, 2010; Seiler *et al.*, 2013a). Despite official protection through government agencies, habitat destruction has continued over the past decade: human-induced forest fires and logging worsened after the 2009 political crisis, severely affecting remaining forests (Seiler, 2012). The Ankarafa Forest in the west of the peninsula (totalling around 300ha in size, Volampeno *et al.*, 2010) remained relatively protected due to the placement of a research site and ongoing presence of researchers, guides and non-governmental organisation (NGO) members (Seiler *et al.,* 2013b). The biggest connected forest in the east of the Peninsula, Analavory, however, has been decimated within the last decade and the remaining unconnected fragments effectively total around 100ha in size (Randriatahina and Schwitzer, personal communication).
In addition to habitat loss, sportive lemurs are hunted for food (Schwitzer *et al.*, 2006; Seiler *et al.*, 2010). Although hunting events were recorded only sporadically (Volampeno *et al.*, 2010), their sessile nature during daylight hours makes sportive lemurs easy prey for opportunistic hunters. These threats call for conservation measures that include long-term population monitoring to assess the effects of habitat loss and hunting on the last Sahamalaza sportive lemur populations. To date, however, the exact range of Sahamalaza sportive lemurs has not been investigated: there remains the possibility that populations exist on the mainland. After initial surveys in 2004, found no evidence of this species on the mainland (Olivieri *et al.,* 2005) it was generally assumed that this species was not represented off the peninsula, but this has not been confirmed since. Given the uncertainty of the species' distribution, it has been difficult to produce a robust population size estimation. Only two population density estimations studies have been conducted to date with a highly variable result: Ruperti (2007) conducted *ad libitum* surveys in one-hectare plots during the daytime over four months, estimating a mean density of 280 individuals/km^2. Seiler (2013a) counted all individuals encountered during three field seasons (totalling up to 12 months between 2009 and 2011), estimating a density of 7 to 23 individuals/km^2. Despite differences in estimations (attributed to habitat alterations and different methodologies; IUCN, 2018) these population density estimations have contributed to the decision of classifying Sahamalaza sportive lemurs as Critically Endangered by the IUCN Red List (IUCN, 2018).
While important for baseline assessments, these highly dissimilar estimations of the remaining populations fail to inform effective conservation-based monitoring. This study therefore aims to 1) determine the exact distribution range of Sahamalaza sportive lemurs off the peninsula, and 2) produce a robust population density estimate using standardised and repeatable methodology.

Methods

Study Sites
Presence/absence surveys were conducted in five forest fragments in the northwest of Madagascar, on the mainland east of the Sahamalaza Peninsula (Fig. 1; Tab. 1). The fragments were chosen as they were located between the rivers Maevarano (in the south) and Andranomalaza (in the

north) (Fig. 1), which are presumed to be natural barriers for sportive lemur speciation (Craul *et al.*, 2007). Data were collected between April and May 2013.

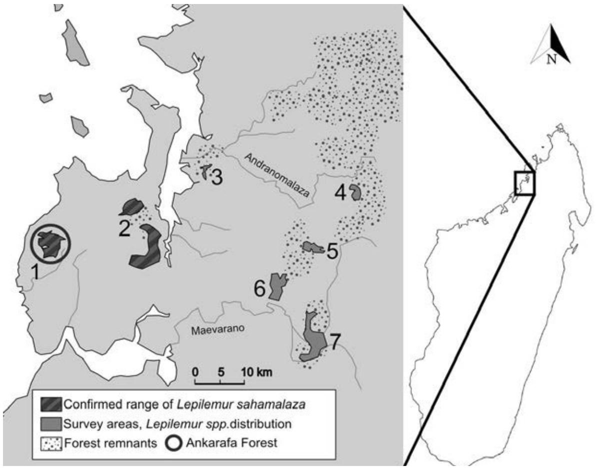

Fig. 1: Location of study sites on the Sahamalaza Peninsula in north-western Madagascar. Study site 1: Ankarafa forest; site 2: Analavory and Anabohazo (sites 1 and 2 make up the Sahamalaza-Iles Radama National Park); site 3: Marovato Sud; site 4: Anefitrabe; site 5: Betolongo; site 6: Andrafiabe; site 7: Sasindro. Transect counts and population density estimations were performed with data collected at site 1. Surveys for absence/presence of sportive lemurs were performed in the mainland areas between the rivers Maevarano (south) and Andranomalaza (north) (sites 3 to 7).

Tab. 1: Names and GPS waypoints of survey areas where presence/absence surveys were conducted in 2013. Location ID numbers correspond with numbers in Fig. 1.

Location ID	Name	Southing	Easting	Survey duration
1	Ankarafa	-14.38019	47.76057	N/A
2	Analavory and Anabohazo	-14.32253	47.91427	N/A
3	Marovato Sud	-14.14397	48.02204	2 days
4	Anefitrabe	-14.1727	48.21424	4 days
5	Betolongo	-14.24404	48.14404	4 days
6	Andrafiabe	-14.29546	48.12187	4 days
7	Sasindro	-14.32394	48.17336	4 days

Data on population density were collected in the Ankarafa Forest within the Sahamalaza – Iles Radama National Park (Fig. 1). The Ankarafa Forest, the most western forest patch within the protected area located between 13°52'S and 14°27'S and 45°38'E and 47°46'E, is characterized by a mix of dry deciduous and Sambirano rainforest vegetation structures with a canopy height of 25m, as is typical for Malagasy lowland forests (Dumetz, 1999; de Gouvenain and Silander, 2003; Grubb, 2003; Volampeno *et al.*, 2013). The climate on the Sahamalaza Peninsula is highly seasonal with a hot and wet period between November and March and a colder dry period between April and October. Data collection took place between March 2015 and August 2016.

Sahamalaza sportive lemur distribution range

Each study location on the mainland was visited for 2-4 days. Surveys were conducted during daytime and night-time. During daytime surveys, we conducted reconnaissance walks, looking for sleeping trees. Night-time surveys were then conducted to detect the nocturnal sportive lemurs, whose presence was identified by movement, vocalization and eye shine. Local villagers were also asked to provide information on known sleeping sites for nocturnal sportive lemurs.

Density Evaluation

For population counts we walked a total of 26.7km across three line-transects situated in three parts of the Ankarafa Forest (Fig. 2). Transect lengths and number of repeats were variable due to weather conditions and accessibility issues during fieldwork: FRAG1 = 2.2km (surveyed 9 times), FRAG2 = 1.3km (surveyed 3 times) and FRAG3 = 1km (surveyed 3 times). As it was not possible to establish parallel and linear transects through the vegetation, non-linear, pre-existing trails that led through each forest fragment were used. Transect walks were conducted between 6:30pm and 10:00pm, when the lemurs were active. Three to five people walked at an approximate speed of 2km/h using torches to detect lemurs. Communication was held at a minimum so as to not disturb the lemurs. Each time a sportive lemur was spotted, and the species confirmed, the following data were recorded at the location the lemur was first seen: time, number of individuals, perpendicular distance from the transect (measured using a laser distance meter: GLM 30, BOSCH Professional) and the coordinates (using a handheld GPSMAP Garmin 60 CSx,). If independence of the sighting was uncertain, it was not recorded again (N = 3). Data were analysed using the software DISTANCE (Thomas *et al.*, 2010).

Home range-based estimation

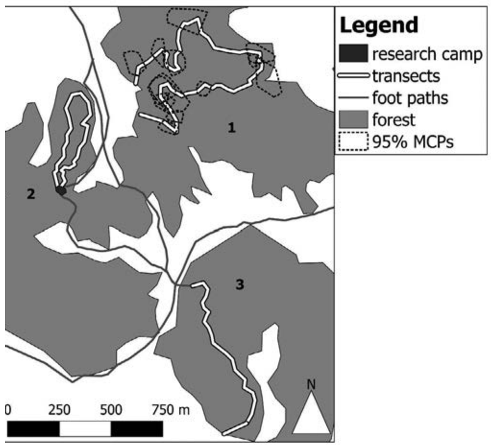

Fig. 2: Line transects surveyed in the Ankarafa Forest (location 1) between 2015 and 2016. FRAG1 = 2.2km, FRAG2 = 1.3km, FRAG 3 = 1km. Dotted lines represent 95% Minimum Convex Polygon (MCP) home ranges of all tagged Sahamalaza sportive lemur individuals.

We fitted 14 Sahamalaza sportive lemurs, inhabiting FRAG1 of the Ankarafa Forest (Fig. 2) with cable-tie VHF radio-collars (3.5g; Biotrack). From October 2015 until August 2016 behavioural observations of these focal individuals were conducted between 6:00pm and midnight. The location of each tree visited by focal individuals was marked by taking a GPS fixture. Fixtures for each focal animal were collated and used to estimate annual home ranges (number/individual mean±SD: 333±134, range = 106 – 587 points). Home range size was calculated for each individual as 95% Minimum Convex Polygons (MCP). Overlap between home ranges of the study individuals was calculated according to the degree of overlap in QuantumGIS (Version 2.18). The area of overlap was expressed as percentage of home range area.

Results

Sahamalaza sportive lemur distribution range

No populations of Sahamalaza sportive lemurs were found outside of the confirmed distribution range on the Sahamalaza Peninsula. Local villagers admitted to knowing of nocturnal lemurs but claimed they were 'very difficult to find'. No *Lepilemur* spp were sighted at any of the survey sites during the survey period.

Density Evaluation

We recorded 200 independent sightings of sportive lemurs throughout the study (FRAG1: 156 sightings; FRAG2: 24 sightings; FRAG3: 20 sightings). The most sightings recorded for one survey night was 27 individuals in FRAG1. Encounter rates varied across survey nights and forest fragments: on average 8.2±2.7 (mean±SD) individuals per kilometre were encountered in FRAG1, 6.4±1.9 individuals per kilometre in FRAG2 and 6.6±1.2 individual per kilometre in FRAG3. Across all forest fragments the population density was estimated to be 1.52 individuals/ha (% coefficient of variation: 21.7).

Home range-based estimation

Home range sizes differed between individuals with variable overlap between direct neighbours (Tab. 2). Based on the average home range size of 0.67ha, population density was calculated as 1.49 individuals/ha. However, home ranges were not exclusive: the average overlap measured between collared individuals in this study was 20.6% (Tab. 2). Adapting the calculation to account for the average overlap between individuals, and assuming the remaining home range was used exclusively, the population density was estimated to be 1.87 individuals/ha.

Tab. 2: Home range sizes (95% MCPs) and overlap of ranges with direct neighbours of all collared study individuals in the Ankarafa Forest. F = female, M = male.

Individual	Home range size (ha)	Percentage overlap (mean±SD)	Number of tagged individuals overlapped with
F1	0.87	35.4±41.5	3
F2	0.31	10.7±7.2	1
F3	0.29	N/A	0
M4	0.93	N/A	0
F5	0.27	12.6±6.7	3
F6	0.25	69.5±0	1
F7	0.79	1.3±0	1
M8	0.40	2.6±0	1
F9	0.57	N/A	0
M10	0.34	2.4±0	1
M11	1.88	14.1±19.8	5
M12	0.73	29.6±0	2
F13	0.18	27.7±14.2	3
M14	1.60	N/A	0
mean±SD	0.67±0.50	20.6±12.7	

Abundance

The total forested area in which Sahamalaza sportive lemurs are reported to occur on the Sahamalaza Peninsula is estimated to be 2,500ha (Schwitzer and Randriatahina, personal communication). Given a population density estimation of 1.52 individuals/ha we estimate the remaining population to be around 3,800 individuals. The slightly higher population density estimation using the home range and overlap data (1.87 individuals/ha) would result in a total population of 4,675 individuals on the Sahamalaza Peninsula.

Discussion

The results of this study support previous reports (Olivieri *et al.,* 2005) that Sahamalaza sportive lemurs do not occur outside of the Sahamalaza Pensinsula, their assumed distribution range. We estimate here that the remaining populations, which are limited to the forested areas on the peninsula, are comprised of 3,800 to 4,700 individuals. The actual size of the remaining forest on the peninsula has not been assessed and needs ground-truthing. The population estimate can then be adapted using the results presented here for population density.

While the population density estimated in this study is higher than that estimated by Seiler *et al.* (2013) who estimated 0.27 individuals/ha, we suggest this is likely due to differences in methodology rather than a genuine increase in population size. Seiler *et al.* (2013) conducted opportunistic searches and recorded all individuals encountered during behavioural observations in 2009 to 2011, rather than using a standardised methodology. The population density estimated in 2007 by Ruperti (2007) was based on a more systematic approach (resting site searches in 1-hectare plots during the day) resulting in similar estimates to those of the present study with 2.8 individuals/ha. Both studies were conducted in the same three forest parts of the Ankarafa Forest as the present study. It is unlikely that the big differences in estimates stem from population fluctuations alone as no major habitat loss occurred in the Ankarafa Forest from 2006 to 2011 and as sportive lemur females give birth to a single young per year (Mittermeier *et al.*, 2010; Hilgartner *et al.*, 2012), rapid population recovery is unlikely. The more systematic approach in this study, which spanned both the wet and the dry season, gives similar results to the study of Ruperti (2007); it is likely that standardised methods give a more robust estimate (Peres, 1999) and that the results of the present study represent a plausible estimate of the population density at Ankarafa Forest

Forest area in Ankarafa has been relatively stable over the past five years and disturbances have been kept to a minimum by the continuing presence of researchers and field guides. As our surveys took place only in Ankarafa, our density estimates are not likely to be representative of the sportive lemurs' entire range. Population estimations produced in this area may therefore be positively biased. Future studies should estimate population sizes in different parts of the Peninsula, such as the Anabohazo Forest where a research site is currently being completed (Randriatahina, 2017).

When comparing home range sizes of the studied population to those of *Lepilemur* spp. populations living in large connected forests, differences are apparent (Campera, pers. comm.). The home ranges we report here are among the smallest home ranges reported for this genus and present an unusually high degree of overlap (see Ganzhorn *et al.*, 2004; Rasoloharijaona *et al.,* 2006; Hilgartener *et al.*, 2012; Dröscher and Kappeler, 2013; Zinner *et al.*, 2013; Seiler *et al.,* 2015; Dinsmore *et al.*, 2016; Wilmet, 2018).

Limited dispersal possibilities, due to the increasingly fragmented nature of the Sahamalaza forests, may have induced high overlap between individuals (Bondrup-Nielsen, 1985) as the habitat may reach carrying capacity. In addition, unusual pelage colorations increased in the studied populations between 2013 and 2016 (Mandl, personal observation). White tail tips, reportedly found in small, genetically isolated lemur populations, may be a sign of increased inbreeding (Eppley and Donati, 2017), and were found on at least seven different individuals during the study period. The spatial isolation and limited dispersal options, and associated genetic and demographic consequences, make the last populations of Sahamalaza sportive lemurs especially vulnerable to extinction. A genetic study that assesses the viability of sportive lemurs and evaluates their tolerance to isolation would greatly inform future conservation efforts as the species becomes restricted to ever smaller forest fragments.

Based on the results we present, we make the following recommendations for long-term conservation planning:

1. Conducting population density estimations based on the numbers of individuals found in Anabohazo and Analavory is necessary. A systematic approach in both the wet and the dry season is important to establish robust numbers. This will allow assessment of the effect of fragmentation and fragment size on population densities.
2. Focussing reforestation efforts on enlarging the available habitat, starting at fragments that may be quickly connected with (comparatively) little effort.
3. Consideration of implementation of translocation schemes for individuals to improve genetic exchange. The Ankarafa population is genetically, and physically, isolated. A study on the genetic status of the last remaining populations would be an important precursor for translocation activities.
4. Ongoing protection of remaining habitat is imperative. Establishing research stations has proven effective in protection forests (e.g. N'goran *et al*., 2012) and close contact with local government authorities is needed to improve infrastructure in the north-west area.

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All procedures were carried out with ethical approval from the University of Bristol's Ethical Review Group (project number UB/14/048) under the revised Animals (Scientific Procedures) Act 1986 and approved by Madagascar's Ministere de l'Environnement, de l'Ecologie, de la Mer et des Forets (MEEMF) and Madagascar National Parks (MNP) who granted permission for the research to be conducted (permit numbers 37/16/MEEMF/SG/DGF/DAPT/SCBT). The authors would like to thank the Association Européenne pour l'Etude et la Conservation des Lémuriens (AEECL) and Guy Randriatahina for helping with coordination and providing information. A heartfelt thank you to all research assistants and guides who made this assessment possible and who helped substantially with the data collection, especially Mr. Urbain, Mme Lucie, Justin and Cyril. We would like to thank Fonds Lopolod III, the Primate Society of Great Britain, the Explorer's Club Student Grant, Pittsburgh Zoo and PPG Aquarium Sustainability Fund, Primate Conservation Inc.; Fresno Chaffee Zoo and Wildlife Conservation Fund, Minnesota Zoo's Ulysses S. Seal Conservation Grant and the Primate Action Fund for their funding.

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Ontogenesis of behaviour in greater bamboo lemurs (*Prolemur simus*) at Ambalafary, eastern Madagascar: a preliminary study during the first four months of life

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Keywords: Ontogenesis, mother-infant association, *Prolemur simus*, Ambalafary

Abstract
Before reaching maturity, young greater bamboo lemurs (*Prolemur simus*) undergo a developmental period characterized by different phases. The objective of this study was to be able to highlight the initial developmental phases of the lives of young greater bamboo lemurs inhabiting the site of Ambalafary in the Brickaville District, eastern Madagascar, during the first four months of their lives. Focal animal sampling was used between October 2015 and January 2016 to record behaviours of the mother and infants simultaneously. We found that during the first month of their lives, the infant greater bamboo lemurs had complete dependence on their mothers and that regardless of the activities undertaken by the infants, direct body contact with the mothers was almost constant. From the second month of life the mother-infant direct body contact was reduced, as the infants began to venture away from their mothers, and manipulation of non-consumable and consumable objects began. Manipulation of non-consumable objects, such as sticks, decreased during the third month and was not observed during the fourth month. Conversely exploration of consumable objects, such as young bamboo leaves or the bamboo stalk, increased each month. Direct body contact with the mothers decreased during the third and fourth months, and some activities, such as feeding and travelling, occurred up to 4m away from the mothers. A greater understanding of behavioural development in young greater bamboo lemurs is paramount in conservation decision-making and population management for this Critically Endangered species moving forwards.

Résume
Avant d'atteindre la maturité, les jeunes *Prolemur simus* présentent une phase de développement caractérisée par différentes phases. L'objectif de cette étude était de pouvoir mettre en évidence les premières phases de développement de la vie des jeunes *P. simus* habitant le site d'Ambalafary, dans le District de Brickaville à l'est de Madagascar, au cours de leurs quatre premiers mois de vie. La méthode utilisée entre octobre 2015 et janvier 2016 était celle de «Focal animal sampling» pour enregistrer simultanément les comportements de la mère et des jeunes. Nous avons constaté que, pendant le premier mois de leur vie, les jeunes *P. simus* était totalement dépendants de leur mère et que, quelles que soient les activités du jeune, le contact physique direct avec les mères était presque constant. À partir du deuxième mois de vie, le contact corporel direct mère-jeune a été réduit, car les jeunes ont commencé à s'éloigner un peu de leur mère et à manipuler des objets non-consommables et consommables. La manipulation d'objets non-consommables, tels que des bâtons, a diminué au cours du troisième mois et n'a pas été observée au cours du quatrième mois. Au contraire, la manipulation d'objets consommables, tels que les jeunes feuilles de bambou ou la tige de bambou, augmentait chaque mois. Les contacts corporels directs avec les mères ont diminué au cours des troisième et quatrième mois et certaines activités, telles que l'alimentation et les déplacements, ont été pratiquées jusqu'à une distance de 4 m de la mère.

Introduction
Compared with other mammals, young primates have a long period of immaturity (Walters, 1987; Pereira *et al*., 2002; Lonsdorf *et al*., 2012) characterized by a period of high dependence (MacKinnon, 2014). Indeed, non-human primates have few innate (or instinctive) behaviours and therefore must learn behaviours in order to master their physical or social environment in order to survive (Nash *et al*., 1982; MacKinnon, 2014). This learning takes place within the protected framework of a social group and is usually through the mother-offspring link because in most cases in primates it is primarily the mothers who provide their offspring with food, heat, transportation and protection (Nash *et al*., 1982). The development of an individual from birth to maturity is gradual and occurs by stage. This is referred to as the ontogenetic trajectory, during which the young primate acquires various learnt behaviours and preferences (Hinde *et al.,* 1976). Ontogenesis is defined as the psycho-physiological construction of the individual as it develops. The study of behavioural development is therefore called ontogenesis of behaviour (Bateson, 1987). An ontogenetic study helps to understand