

Habitat selection and use in the Critically Endangered Sahamalaza sportive lemur *Lepilemur sahamalazensis* in altered habitat

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ABSTRACT: Habitat selection and use by primates is influenced by the trade-off between distribution of foraging resources and predation risk. So far, there are published studies on habitat use for 2 out of 26 sportive lemur species, but none document habitat selection. We studied habitat in home ranges as well as feeding preferences and nightly activity budgets in the Sahamalaza sportive lemur *Lepilemur sahamalazensis*. We describe the habitat structure of home ranges located in 4 forest fragments in Madagascar with varying habitat characteristics after following 8 radio-tagged individuals for a total of 666 h at night. With the limitation of small sample size, our results suggest that Sahamalaza sportive lemurs choose the locations of their home ranges on the basis of different habitat variables, with abundance of sleeping sites and feeding trees as well as tree density and canopy cover being the most important factors. The Sahamalaza sportive lemur is a highly folivorous generalist herbivore, feeding on at least 42 different tree species and preferring the abundant species *Clitoria lasciva*, *Mangifera indica*, *Garcinia pauciflora* and *Sorindeia madagascariensis*. It has prolonged times of resting during its activity periods. Our results imply that despite its habitat selectivity, even the most degraded fragments on the Sahamalaza Peninsula still adequately meet the species' habitat requirements. However, the small extent of the remaining forest and ongoing deforestation, forest degradation and poaching call the future survival of this Critically Endangered species into question.

KEY WORDS: Habitat selection · Feeding ecology · Activity budget · Habitat requirements · Sportive lemur · Critically Endangered

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INTRODUCTION

A species' selection of a habitat can vary according to that species' body mass, diet, sex, age, group size and population density, but also with season, weather variables, or habitat degradation and fragmentation (Clutton-Brock & Harvey 1979, Harestad & Bunnell 1979, Singh et al. 2001, Haskell et al. 2002). Important factors for habitat selection and use in primates are the distribution of resources that a species depends on, combined with the necessity for protection

against predators (Altmann 1974, Rylands 1986, Oates 1987, Defler 1989). Resources that have been shown to affect habitat selection in primates include the availability of sleeping sites (Altmann 1974, Hamilton 1982, Anderson 1984), water (Altmann 1974, Robinson 1986, Chapman 1988, Barton et al. 1992) and food abundance (Terborgh 1983, Zhang 1995, Olupot et al. 1997). In lemurs, diverse habitat characteristics have been suggested to influence habitat selection and use, such as the abundance of food sources like *Canarium* spp. (Burseraceae) for the

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aye-aye (Sterling 1993), insects and fruits as well as gum-producing trees for omnivorous lemurs (Charles-Dominique & Petter 1980, Hladik et al. 1980, Ganzhorn 1988, Corbin & Schmid 1995, Ganzhorn & Kappeler 1996), leaf quality or production of leaves and fruits for folivorous and frugivorous lemurs, and habitat structure for specialised clingers and leapers (Ganzhorn 1992, 1995).

Species living in degraded forests or forest fragments are likely to face reduced food resources, less sleeping or hiding places, and possibly pressure from invasive species (Irwin et al. 2010). Habitat degradation can, furthermore, mean easier access for predators and, thus, increased predation pressure (Estrada & Coates-Estrada 1995, Onderdonk & Chapman 2000, Irwin & Raharison 2009). In studies on lemurs, varying responses towards disturbed habitat were found, with lower, similar, or even higher densities in disturbed compared to only slightly disturbed forest (Petter et al. 1977, Lehman 2007, Schwitzer et al. 2011). Generally, the abundance of food resources seems to be the best indicator of lemur density (Balko & Underwood 2005) and predictor for behavioural changes (Irwin 2007). Habitat alteration has been described to have a larger impact on more frugivorous lemur species (sifakas *Propithecus* spp.; lemurs *Eulemur* spp.; ruffed lemurs *Varecia* spp.) compared to relatively folivorous species (grey bamboo lemur), with frugivorous species additionally being more easily extirpated (White et al. 1995, Merenlender et al. 1998, Irwin & Raharison 2009). Furthermore, the number of lemur species was positively correlated with the number of tree species in a study by Ganzhorn et al. (1997). Lemur species that are ecologically flexible seem to be less affected by habitat alteration than species that rely on specific habitat characteristics or food sources present only in certain forest types (Ganzhorn & Schmid 1998, Andrianasolo et al. 2006, Schwitzer et al. 2007b). Overall, the extent of impact of habitat alteration on a species is manifold and not clearly predictable without knowing the species' feeding ecology and habitat preferences. Therefore, it is critical to know the conservation value of altered habitats for each species and what conditions are needed to sustain viable populations (Irwin et al. 2010).

Sportive lemurs are small nocturnal folivores that occur in high densities throughout the forested periphery of Madagascar and thus appear to be relatively flexible in their ecology. Yet, the majority of species (20 out of 26) in this endemic primate family have been listed as either Endangered or Critically Endangered on the IUCN Red List (Davies & Schwitzer 2013). Aspects of habitat use have been

studied in only 2 sportive lemur species, Milne-Edwards' sportive lemur *Lepilemur edwardsi* and the white-footed sportive lemur *L. leucopus*. Milne-Edwards' sportive lemur was described as a specialised folivore (Martin et al. 1985, Martin 1990), spending on average >70% of its feeding time on leaves and reaching values of 100% during certain seasons (Thalmann 2001). The white-footed sportive lemur spent 50% of its time resting and/or self-grooming and about 30% of the time feeding (Hladik & Charles-Dominique 1974, Russell 1977). Of the feeding time 91% was dedicated to leaves (51% on the leaves of *Alluaudia procera*), 6% to flowers and fruit, and the remainder to latex and bark (Russell 1977). In a more recent study, the white-footed sportive lemur fed entirely on leaves from 2 tree species and 1 vine species, with no changes between seasons (Nash 1998). No study so far has documented habitat selection in sportive lemurs, and it is not known to what extent altered habitats can support *Lepilemur* populations over the long term. To support effective conservation measures for this genus, baseline data on ecology and behaviour and detailed information on the habitat structure that sportive lemurs depend on is urgently needed.

The Sahamalaza sportive lemur *L. sahamalazensis*, recently assessed as Critically Endangered on the IUCN Red List (Davies & Schwitzer 2013), is likely restricted to the Sahamalaza Peninsula in northwestern Madagascar (Craul et al. 2007), an area that has experienced rapid anthropogenic deforestation in recent years. In the Ankarafa Forest, one of the 3 remaining forest areas in the distribution range of the Sahamalaza sportive lemur, there are significant differences in forest structure, namely in tree density, tree height, canopy cover and tree species composition, and in *Lepilemur* density (range: 0.07 to 0.23 ind. ha⁻¹) between forest fragments (Seiler et al. 2013b), thus making it an ideal site to study the habitat selection of a sportive lemur in altered habitat.

We describe important variables underpinning the habitat selection of Sahamalaza sportive lemur and investigate its feeding preferences and nocturnal activity budgets. We defined habitat selection sensu Hutto (1985, p. 458) as

a hierarchical process involving a series of innate and learned behavioural decisions made by an animal about what habitat it would use at different scales of the environment.

Based on our observations during a previous field season (Seiler et al. 2013a), we predicted that the home ranges of Sahamalaza sportive lemurs would be located in areas with higher tree density, greater

canopy cover, higher tree diversity, taller trees and a specific species composition compared to the structure of the overall forest fragments. If the sportive lemurs chose the locations of their home ranges according to these parameters, then the habitat structure in known home ranges should not differ in the aforementioned structural variables between forest fragments, regardless of the structural differences between the fragments themselves. Based on the low metabolic rate of sportive lemurs (Schmid & Ganzhorn 1996, Drack et al. 1999, Ganzhorn 2002) and the high amount of active behaviour during the day (Seiler et al. 2013a), we furthermore predicted that Sahamalaza sportive lemurs would use other food resources in addition to leaves (such as fruits, invertebrates and buds). We expected them to spend most time during the night resting and feeding and to prefer high (>8 m) forest strata, similar to other sportive lemur species (Hladik & Charles-Dominique 1974, Martin et al. 1985, Martin 1990, Nash 1998, Thalmann 2001).

MATERIALS AND METHODS

Study site

The Ankarafa Forest is situated in the UNESCO Biosphere Reserve and national park Sahamalaza–Iles Radama National on the Sahamalaza Peninsula, which is located in the Sofia Region, NW Madagascar (Fig. 1). The park, officially inaugurated in July 2007 and managed by Madagascar National Parks (MNP), includes both marine and terrestrial ecosystems and is the first park that was created under the 'Programme Environnemental III' of the Malagasy government and the World Bank. The climate is strongly seasonal, with a cool, dry season from May to October and a hot, rainy season from November to April. The Ankarafa Forest lies within a transition zone between the Sambirano domain in the north and the western dry deciduous forest domain in the south, harbouring semi-humid forests with tree heights of up to 25 m (Schwitzer et al. 2006).

There are no large connected areas of intact primary forest left on the Sahamalaza Peninsula, and the remaining fragments all show some degree of anthropogenic disturbance

and/or edge effects (Schwitzer et al. 2007a,b). The forests and forest fragments are separated by grassland with shrubs. All forest fragments were in the process of regeneration after significant anthropogenic disturbance to the original forest vegetation over an extended period. We considered them to be at least 35 yr old, based on aerial and satellite images and GIS data (Harper et al. 2007), and to exhibit the key characteristics of post-abandonment secondary forest (Chokkalingam & de Jong 2001).

The Sahamalaza sportive lemur has so far been confirmed exclusively for this area. Other lemur species in Sahamalaza include the blue-eyed black lemur *Eulemur flavifrons*, the aye-aye *Daubentonia madagascariensis*, the western bamboo lemur *Hapalemur occidentalis*, the northern giant mouse lemur *Mirza zaza* and the fat-tailed dwarf lemur *Cheirogaleus medius*. The lemurs of Sahamalaza are highly threatened by increasing and presumably unsustainable levels of hunting, and by forest destruction and degradation, mainly through land conversion for subsistence agriculture (Schwitzer et al. 2006, Seiler et al. 2010, 2012). Owing to their exposed diurnal resting position, Sahamalaza sportive lemurs are easily accessible to 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, as these predators hunt during *Lepilemur* resting periods (Seiler et al. 2013a).

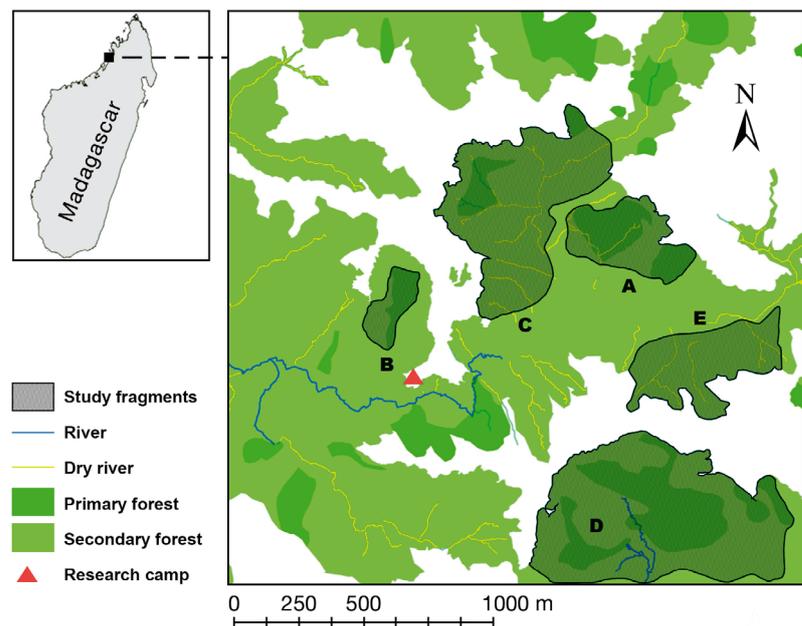


Fig. 1. Study fragments (A–E) and location of research camp in the Ankarafa Forest, Sahamalaza Peninsula, northwestern Madagascar

The Ankarafa Forest, itself highly fragmented, is now one of only 3 remaining forest blocks on the whole peninsula. The remaining forests of the Sahamalaza Peninsula and their unique fauna are in grave danger of disappearing, despite having been under official protection since 2007. The forests are already extremely degraded; nonetheless, bush fires and tree-felling are activities that are routinely pursued and accepted within the local society (Seiler et al. 2010, 2012). In 2010, the Ankarafa Forest measured only about 185 ha, divided into 6 fragments (10, 10, 13, 22, 30 and 100 ha; Seiler et al. 2010). The Ankarafa Forest is home to the Ankarafa research station, the research base for this study.

Activity budget

Four Sahamalaza sportive lemurs were observed during 2 days and nights at the beginning of the first field season in 2009 to construct a basic ethogram of diurnal (Seiler et al. 2013a) and nocturnal behaviours (Table 1). In 2 field seasons (July to October 2009; May to August 2010), 8 individual Sahamalaza sportive lemurs, living in 4 forest fragments, were fitted with radio-collars. 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 syringe projectiles from Telinject. As anaesthetic we used Ketaset 50 (50 mg Ketaset ml⁻¹) in the dose recommended by the manufacturer (0.01 ml per 100 g body mass). Lemurs were anaesthetised for a short period of time for taking body measurements (weight, length of head & body, tail, femur, tibia, foot, forearm, forearm & hand, distance between ears, collection of faecal samples) and equipping with radio collars. Animals were released after recovery at their capture site at the onset of their activity period.

TW3 brass-collar tags and TW3 button cell collars (Biotrack) were used. To make sure that the behaviour of the collared individuals was not altered due to the collar, we observed 5 of them during the day and tested their levels of activity against the level of activity of uncollared individuals, without obtaining significantly different results (Mann-Whitney *U*, *p* = 0.864). A detailed description of the diurnal behaviour of the Sahamalaza sportive lemur, based on 1375 h of behavioral observations on 6 males, 13 females and 26 ind. of unknown sex can be found in Seiler et al. (2013a). During night observations (18:00 to 06:00 h), the radio-collared lemurs were followed and their home ranges were determined using a portable TR-4 receiver (Telonics) during the first season and a Biotrack receiver in the second season, and a 3-element yagi antenna (Biotrack) and a GPS device (GPS 60; Garmin) in both seasons.

For home range habitat analysis, we flagged used and feeding trees of followed individuals. A tree was defined as 'used' when an animal was observed resting in it for at least 10 s and as a 'feeding tree' when we saw the individual feeding on its leaves or fruits. Following the definition of a home range by Burt (1943) as the 'area traversed by the individual in its normal activities of food gathering, mating, and caring for young', only areas with feeding or used trees were included in the analysis. The behaviour of radio-collared individuals and additional information relating to spatial and ecological factors (e.g. height of individual, used tree species, feeding trees, prey) were recorded continuously using focal animal sampling (Altmann 1974). We chose this method as we wanted to avoid missing especially short behaviours of the animals, which are easily overlooked when using an interval observation method. Furthermore, we avoided over- or underestimating shares of different behaviours in the activity budget as we created a

Table 1. Nocturnal ethogram of the Sahamalaza sportive lemur. Only behaviour that was observed during nocturnal observations (18:00 to 06:00 h) is mentioned. The duration of each category was noted in seconds

Behaviour	Description
Resting	Animal sits or lies inactively, eyes closed or opened, but without attentive scanning; or no noise and no movement of the vegetation is detectable at the location of the focal animal.
Vigilance	Animal stops an ongoing behaviour and orients head and eyes toward a specific direction or component of the environment or scans the environment. Eyes are wide open, but small movements can occur.
Feeding	Animal is eating or processing food, or biting and chewing noises are heard at the location of the focal animal.
Locomotion	Animal climbs/jumps up or down a tree and/or jumps to another tree; or movements of vegetation indicate that focal animal advances.
Other	Self-grooming, licking or biting of trees and social behaviour.
Out of sight	Animal is out of sight in canopy and behaviour cannot be classified.

real-time budget. In total, the 8 ind. (1 male, 7 females) were followed 666 h at night: *Lepilemur* (L)1 (male) and L4: 132 h in 11 nights; L3, L5, L6 and L8: 72 h in 6 nights; L2: 60 h in 5 nights; L7: 54 h in 4.5 nights. The percentage of time for which each animal was out of sight was as follows: L1 74 %, L2 46 %, L3 32 %, L4 69 %, L5 46 %, L6 28 %, L7 33 %, L8 47 %. L1, L2 and L3 inhabited Fragment C; L4, Fragment A; L5 and L6, Fragment D; and L7 and L8, Fragment B. No overlap was found between the home ranges of the collared individuals. Animals had an average home range size of 1.4 ha, with the only male animal followed having the largest home range (2.4 ha). The range covered in 1 night was 0.5 ha (Seiler 2012). In total, home ranges of observed animals covered an area of 11.4 ha, equivalent to 16% of the total Ankarafa Forest. A maximum of 32 individual sportive lemurs was found inhabiting the 5 forest fragments (2009: 22, 2010: 32, 2011: 24; Seiler et al. 2013b).

Habitat description of forest fragments and home ranges

For the description of the habitat of each of the 5 forest fragments with confirmed sportive lemur presence we used the point-centred quarter method (Ganzhorn 2003). We took a total of 315 sampling points (63 points per fragment) along 200 to 250 m long transects (6 per fragment). We chose starting points and the direction of transects at random. We located centre points for the point-centred quarter method every 25 m along the transect lines. At each point we measured the distance to the nearest small (5–10 cm diameter at breast height [DBH]) and large (>10 cm DBH) tree for the 4 geographic directions, identified the trees to species or genus level, measured DBH and crown diameter, and estimated their height and bole height. We measured the same parameters for *Bambusa* spp., as this was very abundant in most forest fragments, is a good indicator of degradation and is used by several animal species. This method may overlook rare tree species, but we considered it useful as it allowed a detailed description of large parts of the forest fragments (Ganzhorn 2003).

We calculated the density of trees per hectare as $10\,000/d^2$, where d is the mean distance between the centre point and the nearest tree. We determined canopy cover by taking 1 photograph at each sampling point. The researcher, standing at the sampling point, tilted the camera (Canon Digital Ixus 70; Canon) upwards so that the lens (focal length: 5.8,

focal ratio: 2.8) was pointing straight at the sky. We calculated the percentage canopy cover using the software Metalust (Langel).

We identified trees at least to genus level, using identification guides (Schatz 2001), and existing tree species identifications were carried out by the Département de Flore at Parc Botanique et Zoologique de Tsimbazaza in Antananarivo as part of an earlier study in the same forest fragments (Schwitzer et al. 2007a). We identified 94 % of large trees in Fragment A, 91 % in B, 96 % in C, 96 % in D and 89 % in E. We were able to identify 96 % of small trees in Fragment A, 89 % in B, 96 % in C, 94 % in D and 85 % in E.

We used Simpson's index of diversity to quantify the vegetation diversity of the fragments and home range habitats. The index takes into account the number of species present, as well as the relative abundance of each species. The greater the value (range: 0 to 1), the greater the sample diversity (Simpson 1949).

To describe the habitat in sportive lemur home ranges, the habitat of each previously assessed sportive lemur home range was described using a plot-based method (Ganzhorn 2003). In each home range 8 plots, sized 8×16 m, were randomly chosen, and all large (DBH >10 cm) and small (DBH 5–10 cm) trees within the borders of the plot were described in terms of species, DBH, height, bole height and crown diameter. Canopy cover was calculated by taking 5 photographs at each plot. Furthermore, all suitable sleeping sites (tree holes and tree tangles matching the parameters of preferred sleeping sites; described by Seiler et al. 2013a) within an animal's home range were counted.

Since the forest structure of the fragments was described before the individual *Lepilemur* home ranges were analysed, 5 to 10% of described centre points were located in the home range of observation animals. As additional, unobserved sportive lemurs inhabited the forest fragments and we, therefore, were not able to identify parts of the fragments that were definitely not inhabited by sportive lemurs, we did not exclude the aforementioned points from our analyses. Hence, we compared the habitat of known sportive lemur home ranges with forest fragment structure in general, irrespective of whether it was inhabited by sportive lemurs or not.

Data analyses

To test for differences in structural habitat characteristics between home ranges we used a multivariate

analysis of variance (MANOVA). Where differences between home ranges were statistically significant, we applied multiple Tukey's honest significance tests (Tukey's HSD) as post hoc tests. We had to use 2 different methods to describe forest fragment and home range habitat characteristics, as the home ranges were too small to describe the number of centre points suggested to be necessary for statistical comparison ($N = 50$; Ganzhorn 2003). To test for differences in structural habitat characteristics between fragments and home ranges we used a non-parametric Mann-Whitney U -test. Units of statistical analysis were centre points in the case of the habitat description ($N = 63$ points for each forest fragment) and plots ($N = 8$ for each home range; Fragment A = 8, B = 16, C = 24, D = 16) for habitat descriptions in home ranges. χ^2 tests with Yates-correction were used to compare the frequencies of the 10 most abundant tree species in home ranges, as well as the frequencies of these species being used and fed on, to the same species in the surrounding fragments. The same tests were used to compare the abundance and usage of these tree species between individual home ranges. Numbers of feeding bouts per plant species were used for the analysis. For simplified data presentation we used percentages of the tree species in the results. We used a real time budget to calculate the percentages of time spent on behavioural categories for each individual sportive lemur. We excluded the times spent out of sight to calculate these percentages. As we observed the individuals for varying amounts of time, the percentages are based on the average duration of behaviour per observation hour. For comparisons of behaviour among individual sportive lemurs, we used non-parametric Kruskal-Wallis ANOVA. 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 chosen was 5% ($p \leq 0.05$). Due to the small sample size, we were not able to test activity budgets for differences among fragments. All statistical tests were carried out using SPSS 19.0 (SPSS).

RESULTS

Habitat description of home ranges

For parameters of large trees, MANOVA revealed significant differences between the 8 home ranges of the Sahamalaza sportive lemur (Wilks-Lambda $F = 40853.721$, $p < 0.001$). Differences were found for

density, height and bole height of large trees (Table 2). No differences were identified for DBH, crown diameter, or Simpson's biodiversity index of large trees. However Tukey's HSD identified only 1 homogenous subgroup for the density of large trees ($p = 0.059$). Two subgroups were identified for height and bole height of trees (Table 2).

For measured parameters of small trees, the MANOVA revealed significant differences between the 8 home ranges (Wilks-Lambda $F = 3936.886$, $p < 0.001$). Differences were found for density, DBH and height of small trees between the 8 home ranges. No differences were identified for crown diameter, bole height, or Simpson's biodiversity index for small trees. Tukey's HSD identified 3 subgroups for density of small trees and 2 subgroups for height of small trees (Table 2). Only 1 subgroup was identified for DBH of small trees ($p = 0.059$). Two subgroups were found in the percentage of canopy cover between the different home ranges (Tukey's HSD; Table 2).

There were no significant differences in numbers of available sleeping sites between home ranges (tree hole: 0 to 3 per home range, MANOVA, $F = 0.944$, $p = 0.832$; tree tangle: 14 to 44 per home range, MANOVA, $F = 1.394$, $p = 0.227$), but we counted significantly more tree tangle sleeping sites than tree holes in all home ranges (Tukey's HSD, $p < 0.001$).

Habitat comparison between fragments and home ranges

When directly comparing the habitat parameters of the overall fragments and the 8 home ranges, the density of large as well as small trees was significantly higher in home ranges compared to the overall fragments. The DBH and crown diameter of small trees, but not of large trees, were also significantly higher than in the overall fragments (Table 3).

Table 4 summarises the 10 most abundant tree species in the fragments, in the sportive lemurs' home ranges, as well as their 10 most used and consumed tree species. Overall, the most abundant tree species in the fragments were *Mangifera indica* (9.9%), *Sorindeia madagascariensis* (8.19%), *Grangeria porosa* (6.45%) and *Garcinia pauciflora* (6.11%). *Bambusa* sp. was also very abundant (4.96%), mostly in areas where selective logging was present. The same species were also the most abundant in the home ranges. *M. indica* (23.1%), *S. madagascariensis* (12.47%) and *Bambusa* sp. (8.98%) were also the species most used by the lemurs when resting or moving, and individuals often fed on their leaves. Only in 2

Table 2. Overall canopy cover and density, height, diameter at breast height (DBH), crown diameter, bole height and Simpson's biodiversity index (D) of large (>10 cm DBH) and small (5 to 10 cm DBH) trees in 8 home ranges (1 to 8) located in 4 forest fragments (A–D [see Fig. 1]; median, with Q1–Q3 [quartiles 1 to 3 of the medians] in parentheses; $N = 8$ plots per home range). Medians with different superscripts within a row differ significantly (Tukey-HSD after MANOVA, $\alpha = 0.05$)

	1 C	2 C	3 C	4 A	5 D	6 D	7 B	8 B	F, p
Overall									
Canopy cover (%)	89 ^b (87–92)	87 ^{ab} (79–91)	91 ^b (87–93)	86 ^{ab} (83–90)	89 ^b (84–92)	87 ^{ab} (78–92)	85 ^a (75–86)	82 ^a (67–93)	$F = 13.74,$ $p < 0.001$
Large trees (DBH > 10 cm)									
Density (n ha ⁻¹)	1016 (742–1211)	703 (645–742)	547 (391–703)	469 (273–625)	859 (703–1055)	820 (762–879)	742 (625–801)	469 (449–527)	$F = 3.210,$ $p = 0.006$
Height (m)	12 ^{ab} (11–14)	12 ^{ab} (11–14)	12 ^{ab} (9.6–13)	11 ^{ab} (10–13)	12 ^a (10–13)	11 ^{ab} (9–15)	13 ^b (11–19)	10 ^a (8–12.5)	$F = 2.429,$ $p = 0.030$
DBH (cm)	17.3 (13.4–24.8)	15 (12.3–22.6)	16.7 (13.4–28.1)	14.6 (12.6–19)	15.3 (11.6–20.4)	16.6 (13.1–23.2)	16.4 (13.7–24)	14.3 (11.5–33.4)	$F = 1.357,$ $p = 0.241$
Crown diam. (m)	6 (4.5–8)	6 (5–7)	6 (5–9)	5 (4–6.8)	5.5 (4–7)	5 (4–7)	5 (4–6.3)	5 (4–7.5)	$F = 1.874,$ $p = 0.091$
Bole height (m)	4.8 ^{ab} (2–6.3)	6 ^{ab} (2.9–8.3)	1.9 ^a (0.5–4)	4 ^a (1.2–7)	5 ^{ab} (3–7)	4 ^{ab} (2–8)	8 ^b (3.3–10)	4 ^{ab} (1.9–6)	$F = 4.061,$ $p = 0.001$
D	0.8 (0.7–0.8)	0.9 (0.7–0.9)	0.8 (0.7–1)	1.0 (0.9–1)	0.9 (0.86–0.9)	0.9 (0.8–1)	0.9 (0.9–1)	0.9 (0.8–1)	$F = 0.811,$ $p = 0.582$
Small trees (5–10 cm DBH)									
Density (n ha ⁻¹)	898 ^{ab} (605–980)	820 ^{abc} (762–1191)	1602 ^{bc} (1328–1738)	1523 ^c (1289–2129)	1406 ^{bc} (1328–1719)	859 ^{abc} (742–1250)	586 ^a (430–664)	1250 ^{abc} (410–1680)	$F = 4.625,$ $p < 0.001$
Height (m)	6 ^a (5.5–7.5)	7.8 ^{ab} (7–9.9)	9 ^b (7–10.5)	8 ^{ab} (6–10)	8 ^{ab} (6–10)	7 ^{ab} (5.5–9.8)	8 ^{ab} (6.3–10)	7 ^{ab} (5.9–10)	$F = 2.312,$ $p = 0.038$
DBH (cm)	6.4 (5.4–8)	6.4 (5.7–7.6)	6.1 (5.4–7.3)	6.1 (5.5–7.4)	6.4 (5.4–7.3)	6.8 (6.1–8.3)	7 (6.1–8.3)	5.8 (5.4–7)	$F = 2.355,$ $p = 0.035$
Crown diam. (m)	3 (2.5–4)	3 (2–3.9)	3.5 (3–4.5)	3 (2–4)	3 (2–3.5)	2.5 (2–3)	3 (2.1–4)	3 (2–3.5)	$F = 2.098,$ $p = 0.059$
Bole height (m)	3 (2–4.5)	4 (2.5–5.9)	3 (0.3–6)	4 (2.8–5.5)	4 (3–5.9)	3 (1.5–6)	4 (3–6)	3.5 (2–5)	$F = 0.709,$ $p = 0.665$
D	0.9 (0.88–0.94)	0.9 (0.9–1)	0.8 (0.7–0.9)	0.9 (0.8–0.9)	0.9 (0.8–0.9)	0.9 (0.9–1)	0.9 (0.8–0.9)	0.9 (0.7–1)	$F = 0.839,$ $p = 0.560$

home ranges (5 and 7) was *M. indica* not found among the top 10 species, but still was among the top 10 used and feeding species. In Home Range 7, *S. madagascariensis* was not one of the top 10 tree species, though frequently used and fed on by the sportive lemur. *Garcinia* sp., *Diospyros gracilipes*, *Streblus dimepate* and *Bambusa* sp. were significantly more abundant in home ranges compared to the overall fragments ($df = 1, \chi^2 > 3.84, p < 0.05$; Table 4). *S. madagascariensis*, *M. indica*, *Garcinia* sp., *D. gracilipes*, *S. dimepate* and *Bambusa* sp. were used, and *Garcinia* sp., *G. pauciflora* and *S. dimepate* were fed on significantly more often than expected from the abundance of these species in the overall fragments. We were not able to test differences in abundance of *Clitoria lasciva* as this liana species usually had a DBH < 5 cm and, therefore, was not counted during habitat descriptions. Although the tree species that were

found in all home ranges and were used and fed on by the observed sportive lemurs were mainly the same, their numbers were significantly different between the home ranges, and sportive lemurs were observed to use or feed on these species to different degrees ($df = 1, \chi^2 > 3.84, p < 0.05$ for all).

Overall, we saw sportive lemurs feed on 42 different tree species. Preferred foods were the leaves of the vine species *C. lasciva* (18.69%), followed by *M. indica* (14.13%), *G. pauciflora* (13.48%) and *S. madagascariensis* (9.13%). The sportive lemurs also fed on the fruits of *Ficus tiliaefolia* (0.43%). We only saw them feeding on these fruits twice, and never on fruits of other species. They were also observed eating spiders twice and a beetle once, actively grabbing them off the web and leaves. Once a *Lepilemur* licked and fed on a spiders' web for about 15 min. The proportion of observed folivory was 98.92%.

Table 3. Overall canopy cover, density, height, diameter at breast height (DBH), crown diameter, bole height and Simpson's biodiversity index (D) of large (>10 cm DBH) and small (5 to 10 cm DBH) trees of the fragments and home ranges (median, with Q1–Q3 in parentheses; $N = 63$ centre points per fragment and $N = 8$ plots per home range). Mann-Whitney U -test, $\alpha = 0.05$; significant results are in **bold**

	Fragment	Home range	Z , p
Overall			
Canopy cover	82 (67–89)	87 (82–91)	$Z = -3.986$, $p < 0.001$
Large trees (DBH > 10 cm)			
Density ($n\ ha^{-1}$)	394 (225–674)	703.1 (468.6–858.4)	$Z = -4.927$, $p < 0.001$
Height (m)	11.6 (9.4–13.8)	12 (10–14)	$Z = -1.264$, $p = 0.135$
DBH (cm)	16.7 (13.9–21.3)	15.9 (12.5–23.6)	$Z = -1.467$, $p = 0.142$
Crown diameter (m)	5.8 (4.8–7.3)	5.5 (4–7.5)	$Z = -1.01$, $p = 0.059$
Bole height (m)	4.3 (2.7–5.7)	4.7 (1.8–7)	$Z = 0.707$, $p = 0.479$
D	0.8 (0.8–1)	0.9 (0.8–1)	$Z = 0.171$, $p = 0.863$
Small trees (5–10 cm DBH)			
Density ($n\ ha^{-1}$)	639 (323–1268)	1093.8 (683.6–1562.5)	$Z = -3.786$, $p < 0.001$
Height (m)	7.5 (6–8.7)	8 (6–8)	$Z = 1.493$, $p = 0.067$
DBH (cm)	6.7 (6.1–7.4)	6.4 (5.5–7.6)	$Z = -3.986$, $p < 0.001$
Crown diameter (m)	3.1 (2.8–3.6)	3 (2–4)	$Z = -3.821$, $p < 0.001$
Bole height (m)	3.4 (1.8–4.6)	3.6 (2–6)	$Z = -1.668$, $p = 0.005$
D	0.8 (0.8–1)	0.9 (0.8–0.9)	$Z = 1.401$, $p = 0.122$

Activity budget

In total, the observed individuals rested 47% of the time, were vigilant 23% of the time and fed 18% of the time. Significant differences between individuals were only found for Resting ($p = 0.019$; Table 5) and Other ($p = 0.008$; Table 5). The average height at which the sportive lemurs were sighted was 8.24 m, with significant differences between individuals.

DISCUSSION

Our results, with the restriction of being based on a small dataset of 8 ind., suggest that important habitat parameters in the home ranges of Sahamalaza sportive lemurs are tree density, canopy cover, DBH, bole height and, especially, sleeping site and feeding tree abundance. Since we have not been able to radio-collar every single sportive lemur in the studied forest fragments, comparisons between home range habitat and overall forest fragment structure may include parts of other individuals' home ranges on the fragment side. Nonetheless, since we found higher densities of trees in home ranges than in fragments in general, and since sportive lemur home ranges did not differ from each other in the aforementioned variables between forest fragments (despite the significant differences in forest structure between the overall fragments), our data point towards active habitat selection by the lemurs. Simi-

larly, microhabitats around sportive lemur sleeping sites did not differ within or between forest fragments, irrespective of sleeping site type and habitat structure of the surrounding forest (findings reported by Seiler et al. 2013a).

In a similar study, Pliosungnoen et al. (2010) compared the density and microhabitat selection of the nocturnal Bengal slow loris *Nycticebus bengalensis* between differently degraded habitat types ranging from undisturbed, evergreen tropical forest to *Acacia/Leucaena* plantations of different ages, and found similar loris densities in older plantations and primary forest. The lorises preferred larger and taller trees with large canopies and tended to avoid habitats with little canopy cover. Studies on home range use of 4 capuchin monkey species suggest that the distribution of food sources was the most important factor of habitat choice, but also that differences in forest structure and diversity, water availability and sleeping sites are important elements of the environment (Terborgh 1983, Robinson 1986, Chapman 1988, Zhang 1995). Generally, animals should choose parts of a forest that contain the most essential resources in higher abundances than elsewhere to minimise the energy costs of travelling (Ganzhorn et al. 1997).

A study on blue-eyed black lemurs in the same study area showed that this species used forest fragments of different levels of degradation differently and that the primary forest fragment harboured a higher density of feeding and resting trees; further, the species had smaller home ranges in primary com-

Table 4. Top 10 most abundant tree species in fragments (Fr; N = 2516), home ranges (Hr; N = 1504), as well as the top 10 most used (N = 1091) trees and feeding (Fed; N = 460) trees. Percentages with overall total numbers of each tree species per category are given; the respective number for each category do not add up to the overall value as we only give the top 10 trees here. Top 10 ranks in each category are indicated by superscripts 1 to 10. na: not available (none counted); *Sor.*: *Sorindeia*; *Masc.*: *Mascarenhasia*; *Can.*: *Canarium*

Family	Species	Vernacular	Fr		Hr		Used		Fed	
			%	Overall	%	Overall	%	Overall	%	Overall
Anacardiaceae	<i>Sor. madagascariensis</i>	Sondririny	8.19 ²	213	11.28 ¹	170	12.5 ^{2,a}	136	9.13 ⁴	42
Anacardiaceae	<i>Mangifera indica</i>	Manga	9.9 ¹	247	9.8 ³	89	23.1 ^{1,a}	252	14.13 ²	65
Apocynaceae	<i>Masc. arborescens</i>	Gidroa	3.13 ⁶	82	2.19	31	1.37	15	0.65	3
Burseraceae	<i>Can. madagascariensis</i>	Ramy	2.61 ⁸	62	2.26	32	1.92	21	na	na
Chrysobalanaceae	<i>Grangeria porosa</i>	Morasiro	6.45 ³	165	5.57 ⁵	69	4.49 ⁵	49	5.87 ⁵	27
Clusiaceae	<i>Garcinia pauciflora</i>	Taranta	6.11 ⁴	150	8.53 ⁴	121	9.53 ³	104	13.5 ^{3,a}	62
Clusiaceae	<i>Garcinia</i> sp.	Vavongo	na	na	2.75 ^{9,a}	39	0.92 ^a	10	1.52 ^a	7
Combretaceae	<i>Terminalia perrieri</i>	Lonjo	1.84	45	1.9	27	2.66 ⁷	29	0.43	2
Ebenaceae	<i>Diospyros gracilipes</i>	Hazomainty	0.89	26	2.6 ^{10,a}	37	2.2 ^{8,a}	24	1.3	6
Fabaceae	<i>Clitoria lasciva</i>	Famehyfary	na	na	0.07	1	1.55	17	18.7 ¹	86
Fabaceae	<i>Albizia</i> sp.	Taipapango	1.99	56	2.75 ⁸	36	3.57 ⁶	39	3.04 ⁸	3
Menispermaceae	Unknown	Ambarasaha	1.32	20	1.62	23	2.02 ¹⁰	22	1.52	7
Moraceae	<i>Ficus tiliaefolia</i>	Adabo	2.43 ⁹	47	0.35	3	1.1	12	0.43 ^b	2
Moraceae	<i>Bosqueia</i> sp.	Tsimitombo	1.04	24	2.4	36	0.64	7	1.96 ⁹	9
Moraceae	<i>Streblus dimepate</i>	Tsitindry	1.35	35	4.02 ^{6,a}	62	2.02 ^{9,a}	22	4.78 ^{6,a}	22
Poaceae	<i>Bambusa</i> sp.	Valiha	4.96 ⁵	126	11.2 ^a	160	8.98 ^{4,a}	98	4.38 ⁷	20
Rhizophoraceae	<i>Macarisia lanceolata</i>	Korontsana	3.05 ⁷	71	1.41	20	1.19	13	0.22 ^a	1
Sapindaceae	<i>Macphersonia gracilis</i>	Maroampototro	1.17	27	1.2	17	0.64	7	1.74 ¹⁰	8
Tiliaceae	<i>Grewia amplifolia</i>	Sely	2.39 ¹⁰	62	3.17 ⁷	26	1.65	18	0.43	3
Unknown	Unknown	Hazoambo	1.01	28	0.56	8	1.83	20	1.74 ¹⁰	8

^aSignificantly higher proportionate number of trees of this species in comparison to the overall fragments ($\chi^2 > 3.84$, $\alpha = 0.05$); ^bonly fruit eaten

Table 5. Percentages of feeding, resting, vigilance, locomotion and other behaviours and sighted heights (median plus Q1–Q3 in parentheses) of 8 sportive lemurs (L1 to L8; M: male; F: female). Medians with different superscripts within a column differ significantly (Mann-Whitney *U*-tests with Holms-Bonferroni correction after Kruskal-Wallis ANOVA, $\alpha = 0.05$). Medians for each category are given in the last row

ID	Sex	Feeding	Resting	Vigilance	Locomotion	Other	Sighted height (m)
L1	M	16.7 (11.4–22.1)	53.8 ^{ac} (46.8–62.1)	16.8 (10.9–19.8)	4.1 (3.1–6.9)	1.9 ^{ab} (0.5–4.5)	7.9 ^{ab} (7.2–8.7)
L2	F	26.7 (22.4–47.9)	32.8 ^b (14.5–39.6)	24.4 (16.1–32)	2.8 (1.4–5.4)	1.4 ^{ab} (0.2–3.4)	9 ^{ab} (8.5–9.4)
L3	F	12.5 (9.5–18.3)	46.5 ^{abc} (31.6–62.5)	26.2 (22.9–42.5)	2.8 (2.7–7.5)	3 ^{ab} (2.3–5)	8.8 ^{ab} (8.3–9.6)
L4	F	29.1 (10–30.6)	43.6 ^{abc} (35–55)	23.9 (14.1–33.2)	5.2 (3.6–8.6)	0.6 ^a (0.3–1)	9 ^a (8.7–9.6)
L5	F	14.7 (9.8–20.2)	49 ^{abc} (44.7–54.4)	22.2 (19.7–29.5)	4 (2.4–7.3)	3.3 ^{ab} (1.3–5.6)	6.7 ^{ab} (5.9–7.8)
L6	F	12.5 (8.9–19.9)	46.7 ^{abc} (43.9–53)	29.4 (24.9–38.5)	3.3 (2.6–4.9)	3 ^{ab} (0.8–3.3)	5.9 ^{ab} (4.8–7.3)
L7	F	18.8 (14–25.3)	55.4 ^{ac} (47.5–61.5)	15 (14.5–23.8)	3.2 (1.8–5.1)	0.6 ^a (0.4–1.1)	8.8 ^a (8–9.4)
L8	F	16.5 (7.2–28.2)	34.8 ^{abc} (22.4–54.8)	25.6 (14–41.1)	4.3 (0.7–8.8)	2.6 ^b (1.8–8.3)	6.4 ^b (5.7–7.5)
Test statistics		$\chi^2 = 13.490$, p = 0.061	$\chi^2 = 16.813$, p = 0.019	$\chi^2 = 14.493$, p = 0.043	$\chi^2 = 3.271$, p = 0.859	$\chi^2 = 19.019$, p = 0.008	$\chi^2 = 36.469$, p < 0.001
Median (Q1–Q3)		17.9 (10.4–27.3)	47.3 (33.8–57.2)	23.3 (15–31.9)	3.8 (1.8–7)	1.8 (0.6–4)	8.3 (6.6–9.1)

pared to secondary fragments (Schwitzer et al. 2007b). As Schwitzer et al. (2007b) also found a lower density of blue-eyed black lemurs in the secondary forest fragment, the authors concluded that this type of habitat is only of limited value to the species, which is contrary to our results for Sahamalaza sportive lemurs. The differences between the studies on capuchins (Terborgh 1983, Robinson 1986, Chapman 1988, Zhang 1995) and Schwitzer et al.'s (2007b)

study on blue-eyed black lemurs compared to our results are most likely due to the different feeding types of the study species. Capuchins and blue-eyed black lemurs are mainly frugivorous, and are thus dependent on fruit trees in their home range, whilst the Sahamalaza sportive lemur is a folivore, with a relatively broad spectrum of abundant feeding trees and is thus independent of clumped resources such as fruit trees.

Preferred feeding trees of observed sportive lemurs like *Mangifera indica*, *Sorindeia madagascariensis*, *Grangeria porosa*, *Garcinia pauciflora*, *Streblus dimopate*, *Bambusa* sp. and the liana species *Clitoria lasciva* were significantly more abundant in home ranges and were used and consumed in higher amounts when compared to their overall abundance in fragments, suggesting that home range habitat selection might depend on the distribution of these tree species. *S. madagascariensis*, furthermore, was a preferred sleeping tree species (Seiler et al. 2013a), and its higher abundance in home ranges might be due to this function. Although the tree species that were found in all home ranges and were used and fed on by the observed sportive lemurs were mainly the same, their numbers differed between the home ranges, and individual sportive lemurs used or fed on these species for different amounts of time, suggesting some degree of flexibility. This observation might also be due to the fact that we were not able to observe every feeding event and did not describe every tree in an individual's home range.

A leaf-based diet is generally characterised as low quality due to the difficulties associated with cellulose digestion, the low energy value relative to other diets and the possible presence of secondary compounds that may be toxic or reduce digestibility (Milton 1979). We thus predicted that Sahamalaza sportive lemurs use other food resources in addition to leaves in order to meet their energetic requirements, and we indeed found sportive lemurs occasionally feeding on fruits, invertebrates and even a spider's web. As we did not conduct night observations between December and March, it is possible that sportive lemurs added more fruits to their diet during that time of the year. Ripe fruits of several different tree species were available and regularly fed on by blue-eyed black lemurs during the observation period, however. The amount of invertebrate intake presumably was also higher than we were able to observe, as individuals tended to feed relatively high in the trees, where foraging and feeding on invertebrates was nearly impossible to observe during the night. A follow-up study focusing on the composition of Sahamalaza sportive lemurs' diet, best with the help of faecal analyses, is thus necessary to draw final conclusions on dietary variety. Based on the observations made in this study, we classified the Sahamalaza sportive lemur as almost exclusively folivorous, adding invertebrates to its diet occasionally. Although other sportive lemur species are also known to feed mainly on leaves, values like those observed in the Sahamalaza sportive lemur are only

reached in times of fruit and flower scarcity, as described for the Milne-Edwards' sportive lemur (Thalmann 2001) or the white-footed sportive lemur (Nash 1998).

Following definitions by Dearing et al. (2000) and Freeland (1991), who stated that herbivores can be classified as generalists when they feed on a wide array of tree species or specialists when they only consume one or a few related trees, we classified the Sahamalaza sportive lemur as a generalist herbivore. In comparison to the white-footed sportive lemur, which was described as highly specialised and mainly feeding on only 3 tree species (Nash 1998), the Sahamalaza sportive lemur with at least 42 different feeding tree species can be classified as a generalist. The right composition of the different tree species might, however, be of importance. The similar-sized and nocturnal eastern woolly lemur *Avahi laniger* was described to feed on the leaves of 9 different tree species, with >80% of the diet being comprised of 3 species (Faulkner & Lehman 2006), preferring young leaves with higher protein and protein-to-fiber ratios (Milton 1979, Yeager et al. 1997, Chapman et al. 2004). The eastern woolly lemur has also been observed to use higher quality (high protein, low alkaloid) foods than the weasel sportive lemur *L. mustelinus* (Ganzhorn 1988). Contrary to other *Avahi* species and similar to the Sahamalaza sportive lemur, the southern woolly lemur *A. meridionalis* was described to feed on leaves of 43 tree species, and Norscia et al. (2012) suggested that this lemur seems to cope with the metabolic constraints of the low-quality diet by resting much during the night. The southern woolly lemurs spent 15% of their time feeding, 67% resting, 14% moving and 4% in other activities during their activity period. The same strategy has been suggested for the white-footed sportive lemur (Hladik & Charles-Dominique 1974, Nash 1998), which increased inactivity (50% resting, 30% feeding) in times of thermoregulatory stress (Nash 1998).

Minimising energy expenditure might be of great importance to sportive lemurs. The sportive lemurs' small body size, with a body mass of about 700 g, is problematic, as 700 g has been suggested as the minimum body mass for primates to be able to energetically sustain themselves on a leaf-based diet (Kay 1984). During its resting period, the red-tailed sportive lemur *Lepilemur ruficaudatus* was found to have a markedly reduced metabolic rate (only 40% of Kleiber value), probably to minimise energy expenditure (Ganzhorn 2002). It remains unclear whether all sportive lemur species have a reduced metabolic rate during the day, especially if they have

a high percentage of active behaviours during their resting period, or if their metabolic rate is also reduced during their active period at night. Therefore, energy-saving strategies for the activity period should, nonetheless, also be important for sportive lemurs, as was found in the present study for the Sahamalaza sportive lemur. For all of the individuals observed, resting made up the largest proportion of the activity budget, with nearly 48% (up to 72% when including stationary vigilance), and only 18% of the time was spent on feeding, indicating an energy expenditure minimising strategy similar to those observed in other folivorous primates (white-footed sportive lemur: Hladik & Charles-Dominique 1974, Nash 1998, Warren & Crompton 1998; southern woolly lemur: Norscia et al. 2012; howler monkeys, *Alouatta* spp.: Milton 1978). It has to be taken into account that the considerable amount of resting in a folivorous species might not only represent an energy-saving strategy, but might also be due to the fact that resting is a digestive necessity for these animals. As we were unable to test inter-seasonal differences in amounts of resting, we are not able at this point to clearly discriminate between resting as an energy-saving strategy and as a digestive necessity in the Sahamalaza sportive lemur.

In summary, although the small number of observed individuals makes it hard to draw final conclusions on the habitat selection of the Sahamalaza sportive lemur, our results suggest that the species chooses its home range on the basis of habitat characteristics such as tree density, canopy cover, species composition and the abundance of sleeping sites. The Sahamalaza sportive lemur is primarily folivorous and feeds on a large number of tree species, leaving it relatively unaffected by minimal amounts of habitat degradation, due to a certain degree of flexibility. We suggest that it copes with this low-energy diet by engaging in prolonged phases of resting during its activity periods.

Although the different degrees of habitat degradation in the studied forest fragments did not correlate with the lemurs' behaviour in this study, further degradation is likely to have a negative impact. In previous studies, lemur populations even increased after slight disturbances but declined after severe habitat degradation, an effect that has been suggested to be caused by higher primary productivity at increased light levels in slightly disturbed areas and decline of suitable substrate and food availability at higher disturbance intensity (Ganzhorn 1993, 1994, 1995). Howler monkeys (*Alouatta* spp.) are also known for their ability to

persist in both conserved and disturbed conditions, but a recent study found evidence that they are negatively affected by high levels of habitat loss, fragmentation and degradation, with patch size being the main factor constraining populations in fragmented habitats (Arroyo-Rodríguez & Dias 2010). With a total remaining forested area of 200 ha in the Ankarafa Forest, the largest of only 3 forest areas on the Sahamalaza Peninsula, only little habitat is left for the Sahamalaza sportive lemur. The remaining habitat is very fragmented, and various instances of logging, slash-and-burn agriculture and poaching of sportive lemurs were observed during the study period (Seiler et al. 2010, 2012). Strictly arboreal species such as sportive lemurs, which are unable to cross the non-forest matrix within their distribution range, will eventually become extinct when their habitat patches get too small and disconnected to support a viable gene pool/flow (Frankham et al. 2002, Fahrig 2003). The smallest forest fragment with confirmed sportive lemur persistence has been found to be 6 ha for the red-tailed sportive lemur (Ganzhorn et al. 2000, Gibbons & Harcourt 2009) and 5.4 ha for the Milne-Edwards' sportive lemur (Craul et al. 2009). The smallest fragment where Sahamalaza sportive lemurs were found in this study measured 10 ha.

Although in the short term, the Sahamalaza sportive lemur seems to be able to find adequate home ranges in the remaining forest fragments of Ankarafa, it is very likely that, with ongoing habitat degradation and missing law enforcement, the fragments will soon be degraded to a level or cleared to a degree that the species is unable to cope with. This would ultimately lead to the extinction of this already Critically Endangered species.

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