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Variation in Habitat and Behavior of the Northern Sportive Lemur (*Lepilemur septentrionalis*) at Montagne des Français, Madagascar

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Abstract: Understanding variation in habitat quality, diet, and behavioral patterns is fundamental for the development of conservation strategies for threatened primates. From June−August 2013, we conducted a preliminary study of four northern sportive lemurs (*Lepilemur septentrionalis*)—Critically Endangered, solitary-foraging primates living in different forest fragments in Montagne des Français, Madagascar. We sought to obtain the first systematic data on the behavior and feeding ecology of this species in the wild, and identify potential differences in habitat characteristics. The four individuals in our study are estimated to represent approximately 8% of the known population of this species, about which very little else is known. Our data showed that the variety of plant parts consumed did not differ among the four individuals despite differences in habitat as determined by measures of anthropogenic disturbance, tree density, species diversity, total tree basal area, and presence of invasive species. The data suggest, however, that individuals in areas that suffer more anthropogenic threats spent slightly more time feeding, devoted a greater percentage of feeding time to fruit than to leaves, and had larger home ranges than those in areas with fewer different anthropogenic activities. Our results suggest that the ability of the northern sportive lemur to adjust its behavior under different environmental conditions may be beneficial to their ability to persist in degraded habitats.

Key Words: Behavioral flexibility, conservation, feeding ecology, anthropogenic actions, Madagascar, sportive lemur

Introduction

Habitat fragmentation and degradation are among the greatest threats challenging tropical primates today (Chapman *et al.* 2007; Junge *et al.* 2011; IUCN 2012). Although intermediate disturbance may favor some species, inevitably most species decline in response to forest fragmentation due to food shortage, inaccessibility of mates, or hunting (Ganzhorn *et al.* 1997; Irwin *et al.* 2010). The persistence of a species living in fragmented and degraded habitats depends on its ability to adapt to these altered landscapes (Cristobal-Azkarate and Arroyo-Rodríguez 2007).

Fragmentation has been shown to alter habitat properties that include floristic composition, habitat heterogeneity, interspecific competition, predation pressure, and population density (Marsh 2003; Irwin 2008; Gabriel 2013). In fragmented landscapes there can be variations of habitat quality, defined as the suitability of an environment to provide the necessary elements for survival (Hall *et al.* 1997; Gabriel 2013). Fragmentation and reduced habitat quality are variables that have been shown to influence the behavior and distribution of primates in several ways, including altering activity time budgets, daily path length, home range size, and population density, and, perhaps most importantly, dietary composition (Bicca-Marques 2003; Menard *et al.* 2013; Marsh *et al.* 2016). Understanding the different parameters that influence intraspecific variation in behavior patterns is vital as these are indicators of the capacity of primates to respond to rapid changes in environmental conditions (Strier 2009). Species with a greater degree of behavioral and dietary plasticity will be able to respond better to these changes, contributing to their ability to survive in degraded and fragmented habitats.

Lemurs are small to medium-sized primates, endemic to the island of Madagascar. They exhibit a variety of distinctive physiological, social, morphometric, and demographic features, often referred to as the "lemur syndrome" (Jolly 1998; Wright 1999; Kappeler and Schäffler 2008). Their unique traits include lack of sexual dimorphism, female dominance over males, even sex ratios in social groups, instances of monogamy, and cathemerality (Kappeler 1990; Jolly 1998; Wright 1999; Curtis 2006). These varying and distinguishable features of lemur biology and behavior have been suggested as adaptations for energy conservation during bouts of natural seasonal variability (Wright 1999); however, they may also allow for survival in fragmented and disturbed habitats.

Over 90% of the lemurs are now threatened with extinction; as a group, they are among the world's most endangered vertebrates (IUCN 2012; Schwitzer *et al*. 2013). Madagascar's habitats are under a wide array of anthropogenic threats from a rapidly growing human population. They include internal migration, reliance on crops, introduced invasive species, traditional cultural practices (i.e. slash-and-burn agriculture, pet trade, and ritualistic hunting), illegal logging, poaching, the bushmeat trade, and the expansion of stone and mineral mining (Barrett and Ratsimbazafy 2009; Brown and Yoder 2015). Human-induced land disturbance and the direct hunting of species are widespread, and have been linked to the extinction of at least 15 lemur species over the past few centuries (Mittermeier *et al.* 2010; Gorenflo *et al.* 2011). Although global climate change is expected to seriously affect island ecosystems such as Madagascar (Brown and Yoder 2015), the exact extent is unknown, and the impacts of widespread human actions on the island are of more immediate concern (Irwin *et al.* 2010; Dewar and Richard 2012). As a result, studies to assess the effects of habitat loss and degradation on species diversity and the ability of lemurs to cope with these pressures are of great importance (Mittermeier and Cheney 1987; Lerdaeu *et al.* 1991; Ganzhorn 1995; Marsh 2003; Dunham *et al.* 2008; Irwin *et al*. 2010; Junge *et al.* 2011; Gabriel 2013).

Lepilemuridae is a monotypic primate family of nocturnal, solitarily foraging, folivorous lemurs (Ganzhorn 1993). To date there are published studies analyzing habitat use for only six of the 26 sportive lemur species (Hladik and Charles-Dominique 1974; Warren 1997; Nash 1998; Ganzhorn *et al.* 2004; Seiler *et al*. 2014; Sawyer *et al.* 2015). The present study focused on the northern sportive lemur (also known as the Sahafary sportive lemur), *Lepilemur septentrionalis*, which was reclassified from a subspecies to a full species in 2004 (Ravaoarimanana *et al.* 2004; Rumpler 2004; Andriaholinirina *et al.* 2006). It is Critically Endangered and restricted to two small forest fragments in northern Madagascar, in the Sahafary region and Montagne des Français, an area 12 km southeast of the seaport town of Antsiranana (Ranaivoarisoa *et al.* 2013). These forest patches are under extreme anthropogenic pressure from local people who are harvesting trees to be used or sold as charcoal. Charcoal production in particular, along with other anthropogenic activities such as cattle grazing, agriculture, and development, are responsible for the alteration, fragmentation, and degradation of the northern sportive lemur's habitat in Montagne des Français.

Surveys conducted in 2007 estimated the total population of the northern sportive lemur to be 100−150 individuals; however, data collected in 2011 and early 2012 revealed the presence of only 19 known individuals (Ranaivoarisoa *et al.* 2013). The most recent survey, conducted in late 2012 and early 2013 indicated a slightly larger population of 52 individuals, with 95% of them located at Montagne des Français (Louis and Zaonarivelo 2014). As such, the northern sportive lemur is one of the rarest and least protected lemurs in Madagascar, and perhaps the one closest to extinction (Mittermeier *et al.* 2010). Understanding if the northern sportive lemur is able to adjust its behavior under different conditions in its remaining forest fragments is of vital importance to understanding its ability to adapt. Data on diet and activity budgets of this Critically Endangered species in different habitats can aid in identifying conservation priorities.

We conducted a 2-month field study of the species in Montagne des Français, Madagascar. From June to August 2013, we obtained the first systematic data on the behavior and feeding ecology of this species in the wild, with the goal of beginning to understand the extent to which individual behavior and feeding ecology varies with differences in degrees of fragmentation, degradation, and other forms of human disturbance in their habitat. We selected four previously collared individuals as study subjects. They were living in three forest fragments, each with different levels of anthropogenic pressures. We compared their diets, habitats, ranges, and activity budgets. Specifically, we investigated whether differences in these parameters resembled those found for Scott's sportive lemur (*Lepilemur scottorum*), which, although evidently tolerating selectively logged environments where there is less variety of high-quality foods, were absent from highly disturbed areas (Sawyer *et al.* 2016). Degraded forests and even agroforest ecosystems are not necessarily inimical to the survival of primates, however. Golden-headed lion tamarins (*Leontopithecus chrysomelas*), for example, thrive in old *cabruca* agroforests in Brazil. There cultivated fruit (e.g., jackfruit, mangos and figs) is abundant year round, and the diversity of microhabitats (especially their preferred bromeliad epiphytes) is sufficient for prey foraging and sleeping sites (Oliveira *et al.* 2011).

Methods

Study area

Montagne des Français (12°20'02.7"S, 49°21'21.9"E) is a small region of 5,974 ha in the far northeastern tip of Madagascar about 12 km southeast of the large seaport town of Antsiranana (Fig. 1). The area is characterized by fragmented patches of dry deciduous forest surrounding a calcareous massif. Elevation ranges from 100 to 400 m above sea level. Due to its elevation, Montagne des Français has a higher

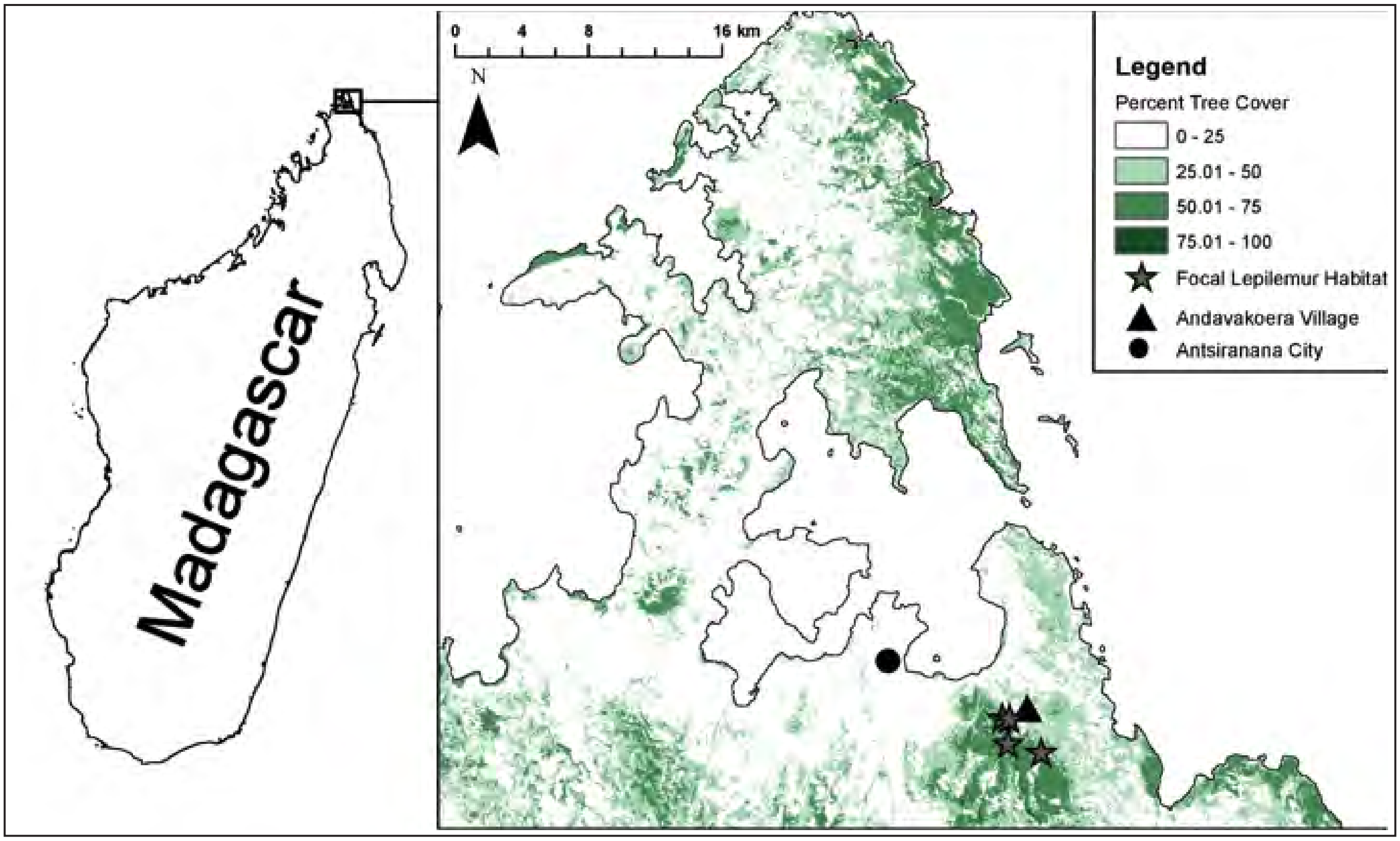

Figure 1. Location of study site in northern Madagascar showing the four habitats of focal individuals and percent of forest canopy cover. Percent forest cover data retrieved from Hansen *et al*. (2013).

annual rainfall than the town of Antsiranana, which receives a mean annual rainfall of 915 mm and nine months of the year are dry (Sabel *et al.* 2009). The wet season is from December to March, and the dry, windy season is from April to November (Robinson *et al.* 2006; Sabel *et al.* 2009). The higher rainfall in Montagne des Français helps support the wide diversity of vegetation and animal life found in the region. In 2008, Montagne des Français was added to the Ramena Special Reserve, officially listed as a government protected area. Montagne des Français is a watershed upon which both local villages and the native flora and fauna depend (Goldstein 2009).

Although protected, Montagne des Français is severely impacted by a number of anthropogenic threats. It no longer consists of contiguous, closed-canopy forest, but has become more of a patchwork of degraded, isolated forests that surround karst mountain peaks (Sabel *et al.* 2009; D'Cruze and Kumar 2011). Years of slash-and-burn agriculture have left this entire region fragmented and scarred by erosion (Ranaivoarisoa *et al.* 2013). People from Antsiranana go into the area to cut down trees for charcoal production and timber. Habitat loss from uncontrolled long-term slash-and-burn practices, regrowth of non-endemic invasive plants, desertification, and hunting are challenges that need to be addressed immediately (Goldstein 2009; Ranaivoarisoa *et al.* 2013). A variety of altered and fragmented landscapes are found at Montagne des Français as a result of these activities (D'Cruze *et al.* 2007; Sabel *et al.* 2009; D'Cruze and Kumar 2011).

Study subjects

Due to limited access and the cryptic nature of the species, only four adults were fitted with radio-telemetry collars (Edward E. Louis Jr. [unpubl. report] following methods described by Louis *et al.* [2006]). In October 2012, the four adult females (coded 'F', 'M', 'O', and 'L') were collared in three forest fragments (individuals 'F' and 'M' were in the same fragment). Beginning in October 2012, they were regularly followed by local Malagasy students to habituate them to human presence. One female ('L') was observed sleeping and associating with an infant (date of birth not known). The three forest fragments inhabited by the focal subjects differed in the extent to which they were degraded by human activities.

Behavioral sampling

Systematic instantaneous scan samples (Altmann 1974) were conducted at 5-minute intervals from 4 June to 1 August, 2013. Visibility of focal individuals varied depending on the level of degradation and canopy cover. Nonetheless, each individual was followed for five consecutive days, for a total of 10 days over the course of this study. Four days of the week, individuals were followed for six consecutive hours beginning at sundown. Scan sampling began at the first indication of movement by the focal individual in its sleep site. On the last day of the week data collection began at approximately 11:00 pm and continued for the next six hours or until the focal subject entered the sleep site for the day. Nine behaviors were recorded in the scans: feeding, resting, moving, autogrooming, social grooming, sleeping, defecating, drinking, and mating. When not seen, they were recorded as out of sight. Here we analyze just the first six behaviors. When feeding, we recorded the plant parts and the Malagasy vernacular names of the plant species. Feeding was recorded only when an individual was observed masticating a food source. Plant parts were categorized as leaves, fruit, vines, new shoots, bark, and flowers.

Ranging and sampling of human activities

At the time of each scan sample, we recorded the location of the focal individual using a handheld GPS (model: Etrex Vista HCx Garmin). GPS points were also collected if an individual moved more than 50 m between scan samples. No points were collected if the individual did not move between scans. We still obtained a GPS reading during a scan whenever the location of the individual was known, even if the animal was out of sight for behavioral observation.

Additionally, we collected GPS points at any sign of anthropogenic activity observed opportunistically while following an individual. These activities included points of logging, slash-and-burn agriculture practices, evidence of hunting, free-ranging zebu cattle grazing, human structures, and crop plantations. These observations were dependent on where the focal individual's movements led us; therefore, anthropogenic activities may have been missed.

Habitat sampling

We set up a 50 m × 20 m plot in each individual's home range to obtain comparative data on tree species composition and density (Tesfaye *et al*. 2013). The initial location of each plot was next to the most used sleep tree. Each plot was located after randomly selecting a direction from the sleep tree, and then broken down into ten, 10 m × 10 m quadrates in which we counted and recorded all trees, measuring the DBH, estimating the height, and noting the vernacular name of each. When samples of leaves, flowers or fruit could not be collected, they were only identified to the genus level. Data were collected only for trees with a DBH >5.0 cm (Irwin 2007; Olson *et al*. 2013). While the DBH cut off in such botanic inventories is generally >10.0 cm, we chose to use >5.0 cm, as *L. septentrionalis* was often observed using trees with a DBH <10.0 cm. Vernacular names were provided by a trained, local guide, and scientific names were determined subsequently. Thirty-six samples (fruits, leaves) were collected in August 2016 and identified by the Department of Botany at the Parc Botanique et Zoologique de Tsimbazaza in Antananarivo, Madagascar. No specimens of leaves or fruits were collected for trees which were easily identified by Masters students from the University of Antsiranana. We also recorded presence/absence of tickberry, *Lantana camara* (Verbenaceae), in each subplot. *Lantana camara* is an exotic invasive species that is often present in secondary forest thickets (Irwin *et al.* 2010). Secondary thickets develop when forests are disturbed and cleared and the land is cultivated and subsequently abandoned, allowing exotic shrubs to invade. Most remaining native elements are widespread species adapted to clearings and edges (Lowry *et al.* 1997; Irwin *et al.* 2010).

Data analyses: habitats

Forest fragments were characterized as more or less degraded by their species diversity, tree densities, total basal area (TBA), mean basal area (MBA), anthropogenic disturbances, and the presence of *Lantana camara*. Based on the presence and severity of each of these factors in each individual habitat, we established a habitat gradient (more degraded to least degraded). This allowed us to make comparisons in behavioral traits for those individuals found in different habitat types.

Plant diversity was determined by calculating the Shannon-Wiener diversity index (H') for each focal individual's home range (Krebs 1989; Rovero *et al.* 2012; Tesfaye *et al.* 2013). Higher values of H' were indicative of a more evenly distributed and diverse habitat. Calculations of the total basal area (TBA) (m^2/ha) and mean basal area (MBA) (m^2) for each plot indicated stand density, and were used to compare stature and biomass of different habitats. Habitats were considered to be more altered if they had a greater number of anthropogenic disturbances present, and a higher percentage of *Lantana camara* present in each habitat plot.

Data analysis: behavior

We determined the activity budget of each individual by combining all observations of a focal individual and calculating a proportion for each behavior. The behaviors collected during scan intervals were combined into five categories: feeding, resting, moving, sleeping and grooming/socializing (including autogrooming). The difficulty in seeing these cryptic lemurs and the visual limitations imposed by their nocturnal behavior meant that focal individuals were sometimes scored as "out of sight." Out of sight records, which ranged from 12.5−34.7% of observations for the four focal subjects, were excluded from the analysis so we could compare the behavior of individuals when directly observed.

To compare the composition of the diets of the individuals in different habitats, we calculated the proportions of different plant parts and species consumed by each. We also measured the food selection ratio for different food species in the diets of each focal individual (a rudimentary indicator of preference). This was calculated by dividing the percentage of time spent feeding on species *i* by the percentage species *i* was found in the plots and presumed to be available to that individual (Chapman and Chapman 2002; Tesfaye *et al*. 2013). A higher selection ratio value is indicative of a more selected species.

Individual home range areas (ha) were calculated using fixed kernel UD and kernel area tests in the R-package

AdehabitatHR. Choosing an appropriate smoothing parameter is the most important aspect when using fixed kernel methodology for analyzing home ranges (Silverman 1986; Worton 1995; Campera *et al*. 2014). While LSCVh (Least squares cross-validation) is the generally favored method, it can provide poor results with small samples sizes (Horne and Garton 2006; Campera *et al.* 2014). As such, data were analyzed using a specified, uniform smoothing parameter given by the LSCVh (h = 11.37), but were not run with LSCVh methods. Kernel area results were compared with area estimates from GPS points in ArcMap 10.3. Home range was evaluated at 95% contours while core areas were evaluated at 75% and 50% contours (Laver and Kelly 2008).

Due to the very small sample size of focal individuals (N = 4), additional statistical tests could not be conducted. Although the sample size is very small, the focal individuals represent approximately 8% of the estimated population of this species.

Ethical note

Our observational research was noninvasive and was conducted under the University of Wisconsin-Madison's Animal Care Waiver for Observational Studies and was in compliance with Malagasy law. The four focal individuals were darted and captured to equip them with radio-collars prior to this study (October 2012) and covered under a separate permit to E. E. Louis Jr. (permit no: 155/12/MEF/SG/DGF/DCB.SAP/SCB) under the Institutional Animal Care and Use Committee #12-101. Individuals were immobilized using a CO_2 remote capture MJ Model DanInject rifle and PneuDarts using 10 mg/ml of Telazol®. These darting methods and the protocol followed those described in Louis *et al.* (2006).

Results

Habitat

Tree density, tree basal area (MBA and TBA), tree diversity, and recorded disturbances varied greatly between each 50 m × 20 m plot. Habitat for individual 'O' had the lowest TBA, tree diversity, and species richness, and the highest indices of *L. camara* and other disturbances (Fig. 2; Table 1). The habitats of the remaining individuals, showed similar tree diversity, but the other parameters varied. Although the habitat of individual 'L' had the highest tree density, it had the lowest MBA. It is important to note that the last two subplots of the habitat of "L" fell slightly outside the individual's home range; these subplots had the highest tree density and lowest MBA in the overall plot. The area had no *L. camara*, and the lowest number of disturbances. It was expected that the habitat of 'F' and 'M' would be similar, as they inhabited the same forest fragment. Both these areas had two types of disturbance present (Fig. 2), and higher MBA and TBA values compared to 'L' and 'O'; however, MBA for 'M' was almost double that of 'F', and TBA was also much higher.

From 67 to 93 home range points were collected on the four focal subjects (Fig. 2). Fixed kernel area analyses indicated that individuals in areas with more anthropogenic activities had larger home ranges. Individual 'F' had the largest home range (95% contour), approximately 2× that of individuals 'L' and 'M' (Table 2). Core areas (50% contour) were more uniform among three of the individuals; however, individual 'F' still had a core area approximately 2× that of the others (Table 2). Individual home ranges varied from 1.32 to 2.90 ha.

The percentage of each tree species per individual plot was highly variable (Table 3). Although 'O' did not have the lowest density (but did have the lowest species richness),

Table 1. Habitat variables and disturbance parameters in each habitat plot in Montagne des Français, Madagascar, June−August 2013.

	Individual lemurs			
Habitat variable	**F**	**O**	**L**	**M**
Tree density (trees/ha)	2,960	2,200	6,750	2,190
Mean basal area (m^2)	0.097±0.79	0.046 ±0.083	0.04±0.13	0.19±1.09
Total basal area (m^2/ha)	288.53±40.77	100.7±2.51	219.69±11.68	411.27±67.26
Diversity (Shannon-Wiener index, H')	2.99±0.07	2.09±0.11	2.60±0.09	2.77±0.08
Tree species richness (species/ha)	40	20	29	33
Invasive (no. of subplots w/ *L. camara*)	3/10	10/10	0/10	0/10
Disturbance (no. of sign types)	2	4	1	2

Table 2. Home and core ranges (ha) of individual lemurs in Montagne des Francais, Madagascar, June−August 2013.

	Individual lemurs			
	F	**O**	**L**	**M**
95% fixed kernel range (ha)	2.90	1.94	1.32	1.49
75% fixed kernel range (ha)	1.44	0.84	0.71	0.78
50% fixed kernel range (ha)	0.68	0.35	0.39	0.34

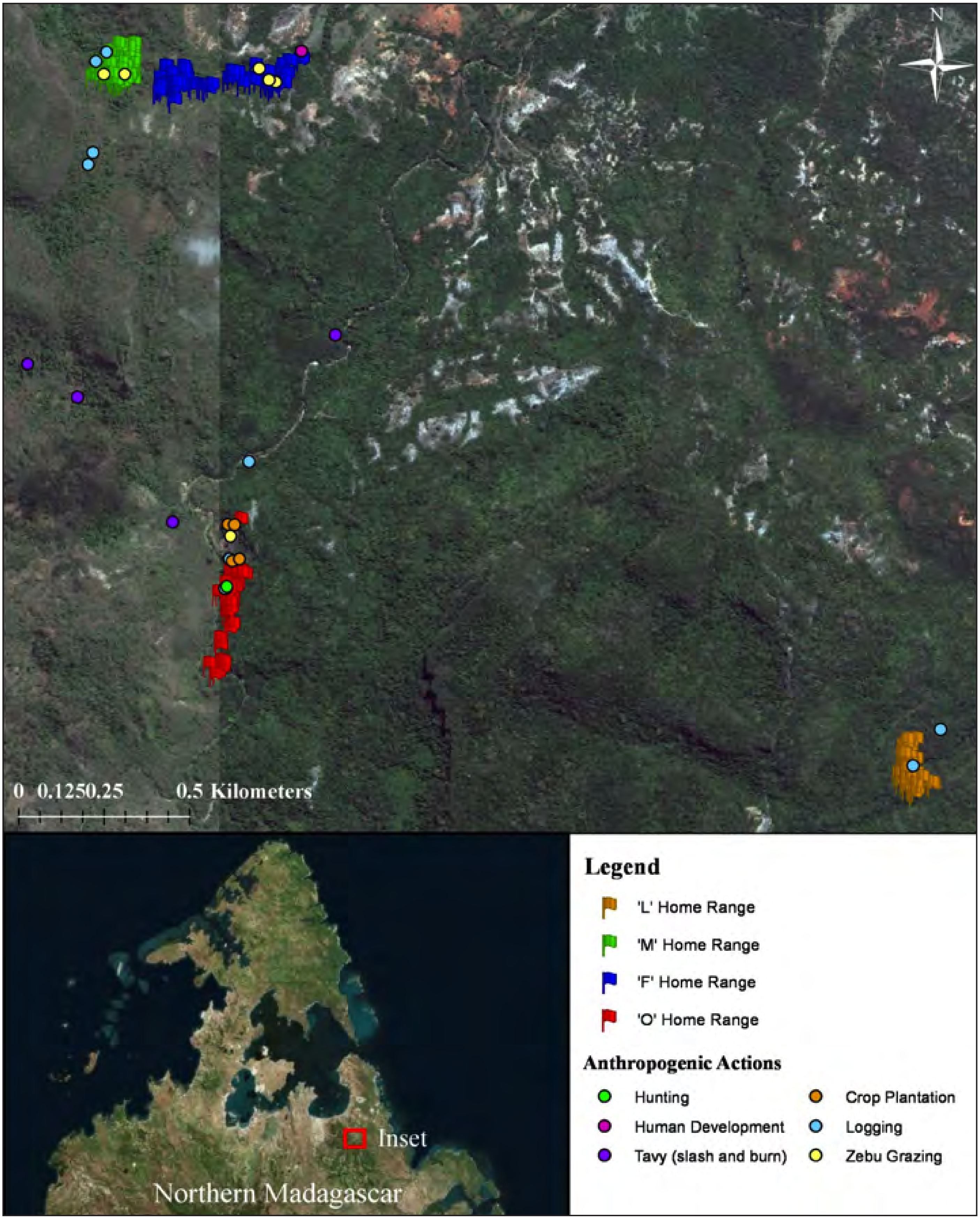

Figure 2. Anthropogenic disturbances and home range points for focal individuals in Montagne des Français, Madagascar, June−August 2013.

Table 3. Overall percentage of individual plant species within each habitat plot in Montagne des Français, Madagascar, June−August 2013.

		Individual Lemurs			
Scientific name	**Vernacular name**	**F**	**O**	**L**	**M**
Albizia lebbeck	Bonarabe	0.68	0.91	-	-
Albizia polyphylla	Hazomborogo/ Fagnamponga	0.34	-	-	-
Annona sp.	Konokono	-	0.45	-	0.91
Antidesma petiolare	Taindalitry	20.27	-	-	5.02
Artocarpus sp.	Finesy	-	-	-	2.28
Brexia sp.	Tsimiranjagna	1.35	-	-	0.46
Canarium sp.	Ndramy	2.36	-	-	9.13
Caesalpinia sp.	Ritro	1.69	3.18	0.30	0.46
Cephalocroton leucocephala	Vahimavo	0.34	-	2.67	1.83
Coffea sp.	Kafe Ala	0.34	-	0.74	0.46
Commiphora lasiodisca	Matambelona	0.34	-	1.04	2.74
Coptosperma sp.	Taolanosy	0.34	-	5.33	-
Cryptostegia madagascariensis	Lombiry	5.74	-	-	-
Delonyx sp.	Folerabonane	-	32.27	-	-
Diopsyros mapingo.	Mapingo	-	-	0.44	-
Diopsyros sp.	Jobiampototro	-	-	2.07	2.74
Dombeya sp.	Tavoa	1.83	-	-	-
Dracaena reflexa	Hasigny	-	-	-	0.46
Elaeodendron sp.	Matifioditra	-	0.91	-	-
Erytroxylum platycladum	Tapiaka	1.35	-	-	-
Fernandoa madagascariensis	Sombotsoy/ Sombitsohy	-	-	-	0.91
Ficus grevei	Mandresy	0.34	-	-	-
Ficus sp.	Voara	0.34	-	-	0.46
Grewia triflora	Sely	13.18	0.45	10.96	-
Jatrofa sp.	Valavelona	5.74	-	-	5.48
Landolphia tenuis	Vahegny	0.68	-	-	-
Leucaena leucocephala	Bonaramatsigny	0.34	20.00	-	1.37
Macpherson ia	Somtororagna	1.69	2.27	22.07	-
Mangifera indica	Manga	-	-	-	1.83
Mascarhenasia sp.	Barabonja	-	-	-	2.74
Moringa oleifera	Agnamorongo	-	0.91	-	-
Maytenus fasciculata	Vahompy	2.03	-	4.74	0.46
Maytenus linearis	Tsimboagnandrefa	0.68	-	-	-
Monanthotaxis boivinii	Fotsiavadiky	3.38	-	-	5.02
Neobeguea ankaranensis	Gavoala	-	1.36	0.89	-
Olax antsirananensis	Kombimba	-	0.45	1.48	-
Olax dissitiflora	Hazotomendry	0.34	-	2.22	-
Pentachlaena sp.	Tamenaka	-	-	-	0.46
Physena sessiliflora	Rasaonjo	-	20.00	6.37	-
Phyllanthus sp.	Mantsikiriva	9.12	-	-	1.37
Pittosporum sp.	Maimbovitsiky	0.68	-	-	-
Poupartia coffra	Sakoagna	-	-	-	0.46
Poupartia sp.	Sakoadihy	2.36	-	-	-

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Table 3. *continued from previous page*

Scientific name	Vernacular name	Individual Lemurs			
		F	O	L	M
Protorhus oblongifolia	Tsy maty magnota	0.34	-	-	-
Rourea orientalis	Magnary	-	-	0.15	1.83
Secamone sp.	Vahilombiry	2.36	-	0.15	-
Senna occidentalis	Sambaravatsy	4.39	8.18	-	-
Sorindea sp.	Sonjiry	2.03	-	4.44	16.44
Strychnos madagascariensis	Vakakoana	-	-	0.30	-
Syzygium sp.	Rotro	2.03	-	9.78	-
Tamarindus indica	Madiromatsiko	-	0.45	3.41	-
Tannodia sp.	Hazodomoy	-	-	1.48	-
Terminalia crenata	Mantaly	-	-	0.89	-
Thespesia gummiflua	Varoala	1.01	-	-	-
Trema sp.	Angezoko	-	0.45	-	-
Trilepisium madagascariense	Lonjo	2.03	1.36	3.11	10.50
Xanthocercis madagascariensis	Voankazomelako	-	1.82	0.30	-
	Unknown Species (multiple)	4.73	2.27	14.07	19.18
	Avocado	-	-	-	0.46
	Gavo	0.68	-	-	-
	Kiranzabmiavy	-	-	0.15	-
	Lavanana	1.69	1.36	-	-
	Mampingo	0.34	-	-	-
	Orange	-	-	-	0.46
	Paiso	-	-	-	0.91
	Pibasy	-	-	-	0.46
	Rotrobentiana	-	0.91	0.15	-
	Sarylombaka	1.01	-	-	-
	Tangegny	0.34	-	-	0.46
	Tsymagnotry	-	-	-	0.46
	Vahy	0.68	-	-	-
	Vahimalimy	-	-	0.15	-
	Vesoala	0.34	-	-	-
	Vontoka	-	-	0.15	-

three species (*Leucaena leucocephala*, *Delonyx* sp., and *Physena sessiliflora*) constituted 72.3% of total trees in the plot. This is reflected in the Shannon-Weiner Diversity index, as 'O' had the lowest H' value (Table 1). The other plots had a more distributed plant species composition. The top three species in the habitat of 'F' (*Antidesma petiolare*, *Grewia triflora*, and *Phyllanthus* sp.) constituted 42.6% of the trees. In the plot of 'L'', the top three species (*Macpherson ia*, *Grewia* sp., and an unidentified species) made up 47.1% of total trees counted, while in habitat of 'M' the top three species (*Sorindea* sp., and *Trilepisium madagascariense*, and an unidentified species) made up 46.1% of all trees within the plot. This is reflected in the comparable H' diversity indices of 'F', 'M', and 'L' (Table 1).

Activity budget

Activity budgets were similar for all individuals (Table 4). While 'F' and 'O' spent less of their observed time feeding than 'L' and 'M', the difference was marginal. A similar result was found when comparing the percentage of time moving. Again, individuals 'F' and 'O' spent more of their time moving than 'L' and 'M', although the differences are slight. The percentage of time resting did not vary between individuals.

Dietary composition and selectivity

While the percentage of time spent feeding per individual did not differ greatly between the four individuals, the composition of what each consumed differed (Table 5). Individuals

Table 4. Overall percentage of activity budget behaviors per individual lemur in Montagne des Français, Madagascar, June−August 2013

	Individual lemurs			
Behavior	**F (N = 479)**	**O (N = 558)**	**L (N = 611)**	**M (N = 585)**
Feeding	13.36	12.01	14.73	15.55
Moving	15.45	13.62	9.98	11.45
Resting	63.68	64.51	64.48	62.91
Grooming/Socializing	6.05	5.38	5.24	6.67
Sleeping	1.46	4.48	5.57	3.42

Table 5. Overall percentage of time spent feeding on specific plant parts per individual lemur in Montagne des Français, Madagascar, June-August 2013.

	Individual lemurs			
Type of food	**F (*N* = 64)**	**O (*N* = 67)**	**L (*N* = 90)**	**M (*N* = 91)**
Leaves	78.13	77.61	87.79	81.32
Fruit	17.19	19.40	1.11	4.40
Flower	1.56	-	-	14.29
New Shoot	3.13	1.49	6.67	-
Vine	-	-	4.44	-
Bark	-	1.11	-	-

in areas with more anthropogenic activities and *Lantana camara* (individuals 'F' and 'O') consumed a lower percentage of leaves (78.1% and 77.6%, respectively) and a higher percentage of fruit (19.4% and 17.2%, respectively) than the other focal subjects (Table 5). Conversely, individuals 'L' and 'M' consumed a higher percentage of leaves (87.8% and 81.3%, respectively) and a much lower percentage of fruit (1.1% and 4.4%, respectively) (Table 5). Individual 'M' spent a higher percentage of her time consuming flowers (14.3%) compared to the other females (Table 5).

Individual 'F' consumed a total of 15 plant species, with *Ficus* sp. (34.35%), *Grewia triflora* (14.1%), and *Landolphia tenuis* (14.1%) as the top three most consumed, accounting for 62.5% of her feeding records (Table 6). 'O' consumed nine plant species in all, with *Grewia triflora* (23.9%), *Tamarindus indica* (23.9%), and *Leucaena leucocephala* (16.4%) being the top three most consumed, accounting for 64.2% of her total diet (Table 7). 'L' consumed items of a total of 12 plant species, with *Tamarindus indica* (26.7%), *Trilepisium madagascariense* (18.30%), and *Tannodia* sp. (14.4%) the top three species, accounting for 59.4% of her overall diet (Table 8). Individual 'M' consumed items from a total of 14 plant species, with *Leucaena leucocephala* (42.9%), *Mangifera indica* (24.2%), and *Tamarindus indica* (13.3%) as the top three most consumed plant species, accounting for 80.23 % of her overall diet (Table 9).

Individuals 'F' and 'O', were most selective for *Rourea orientalis* (313; Table 6) and *Cephalocroton leucocephala* (889; Table 7), respectively. Individual 'L' was most selective for *Paederia argentea* with a ratio value of 1111 (Table 8). This was the second most selected species for individual 'M' with a ratio value of 330. Individual 'M' had the highest selectivity for *Tamarindus indica* with a ratio value of 1319 (Table 9). This species also contributed greatly to the overall diet of individuals 'O' and 'L', but with lower selection ratios.

Discussion

The forest fragments inhabited by the four focal individuals differed considerably in vegetation composition and the number and types of anthropogenic activities. Yet, despite these habitat differences (number of types of disturbance, tree density, TBA, MBA, diversity, and the presence of *L. camara*) the lemurs' overall activity budgets were quite similar. Individuals in habitats with more anthropogenic activities spent less time feeding and more time moving than those in habitats with fewer anthropogenic activities, but the differences were marginal. Individuals in all forest fragments also consumed similar numbers of species.

While these individuals living in different forest patches showed similar activity budgets and types of food species consumed, they varied in the percentage of time they spent feeding on different plant parts. Individuals 'O' and 'F' spent less time eating leaves and more time eating fruit, while 'L' and 'M' spent a much lower percent of their time consuming fruit. It is not clear, however, whether these differences are due to differences in the availability of leaves versus fruits in their respective habitats, which could be more pronounced during the dry season. Individuals with the highest percentage of feeding time on fruit consumed just two species each, one of which, *Grewia triflora*, was eaten by both. The three species chosen for their fruit also contributed to a large percentage of total leaves consumed by these individuals. The selection ratio was moderate for the two species consumed by 'O' while 'F's selection ratio was high for one of the fruit species she consumed. This could suggest that lemurs that did

Table 6. Overall percentage of time spent by individual 'F' on specific plant parts (N = 64) and selection ratio for each species consumed at Montagne des Français, Madagascar, June−August 2013

Scientific name	Local name	Type	Percent of diet				Selection ratio
			Leaves	Fruit	Flowers	New shoots	
Leucaena leucocephala	Bonaramatsigny	Tree	3.13	-	-	-	3
Senna ocidentalis	Sambaravatsy	Tree	3.13	-	-	-	1
Rourea orientalis	Magnary	Tree	3.13	-	-	-	313
Ficus sp.	Voara	Tree	20.30	14.05	-	-	101
Monanthotaxis boivinii	Fotsiavadiky	Tree	1.56	-	-	-	1
Grewia triflora	Sely	Tree	10.94	3.13	-	-	1
Tamarindus indica	Madiromatsiko	Tree	1.56	-	-	-	156
Mangifera indica	Manga	Tree	-	-	1.56	-	156
Ziziphus jujuba	Lamoty	Tree	1.56	-	-	-	156
Maytenus linearis	Tsimboagnandrefa	Tree	9.38	-	-	-	6
Caesalpinia sp.	Ritro	Vine	7.81	-	-	-	5
Landolphia tenuis	Vagheny	Vine	10.94	-	-	3.13	21
Cephalocroton leucocephala	Vahimavo	Vine	1.56	-	-	-	156
Entada leptostachya	Vahintsikidy	Vine	1.56	-	-	-	156
Paederia argentea	Vahivola	Vine	1.56	-	-	-	156

Table 7. Overall percentage of time spent by individual 'O' on specific plant parts (N = 67) and selection ratio for each species consumed at Montagne des Français, Madagascar, June−August 2013

Scientific name	Local name	Type	Percent of Diet				Selection ratio
			Leaves	Fruit	Flowers	New shoots	
Morenga olifera	Agnamorongo	Tree	8.96	-	-	-	10
Leucaena leucocephala	Bonaramatsigny	Tree	14.93	-	-	1.49	1
Senna occidentalis	Sambaravatsy	Tree	1.49	-	-	-	1
Grewia triflora	Sely	Tree	8.96	14.93	-	-	53
Tamarindus indica	Madiromatsiko	Tree	19.40	4.48	-	-	53
Xanthocercis madagascariensis	Voankazomelako	Tree	2.99	-	-	-	2
Cephalocroton leucocephala	Vahimavo	Vine	7.46	-	1.49	-	895
Caesalpinia sp.	Ritro	Vine	5.97	-	-	-	2
Landolphia tenuis	Vahegny	Vine	7.46	-	-	-	746

Table 8. Overall percentage of time spent by individual 'L' on specific plant parts (N = 90) and selection ratio for each species consumed at Montagne des Français, Madagascar, June−August 2013.

Scientific name	Local name	Type	Percent of diet				Selection ratio
			Leaves	Fruit	New shoots	Vines	
Leucaena leucocephala	Bonaramatsigny	Tree	8.89	-	-	-	889
Grewia triflora	Sely	Tree	-	-	5.56	-	1
Tannodia sp.	Hazodomoy	Tree	14.44	-	-	-	10
Trilepisium madagascariense	Lonjo	Tree	17.78	-	1.11	-	6
Tamarindus indica	Madiromatsiko	Tree	25.56	1.11	-	-	8
Syzygium sp.	Rotro	Tree	1.11	-	-	-	1
Macpherson ia	Somotroragna	Tree	1.11	-	-	-	1
Strychnos madagascariensis	Vakakoana	Tree	1.11	-	-	-	4
Olax dissitiflora	Hazotomendry	Tree	1.11	-	-	-	1
Secamone sp.	Vahilombiry	Vine	4.44	-	-	3.33	52
Paederia argentea	Vahivola	Vine	11.11	-	-	-	1111
		Epiphyte	1.11	-	-	1.11	222

Table 9. Overall percentage of time spent by individual 'M' on specific plant parts (N = 91) and selection ratio for each species consumed at Montagne des Français, Madagascar, June−August 2013.

			Percent of diet			
Scientific name	**Local name**	**Type**	**Leaves**	**Fruit**	**Flowers**	**Selection ratio**
Leucaena leucocephala	Bonaramatsigny	Tree	41.76	1.10	-	31
Senna occidentalis	Sambaravatsy	Tree	3.30	-	-	2
Monanthotaxis boivinii	Fotsiavadiky	Tree	1.10	-	-	1
Grewia triflora	Sely	Tree	1.10	-	-	110
Rhopalocarpus sp.	Lombiry	Tree	2.20	-	-	220
Rhopalocarpus undulatus	Lombiry Ala	Tree	1.10	-	-	110
Trilepisium madagascariense	Lonjo	Tree	3.30	-	-	1
Tamarindus indica	Madiromatsiko	Tree	9.89	3.30	-	1319
Mangifera indica	Manga	Tree	9.89	-	14.29	13
Pentachlaena sp.	Tamenaka	Tree	1.10	-	-	110
Cephalocroton leucocephala	Vahimavo	Vine	1.10	-	-	1
Landolphia tenuis	Vahegny	Vine	1.10	-	-	110
Paederia argentea	Vahivola	Vine	3.30	-	-	330
	Vahy	Vine	1.10	-	-	110

consume more fruit were seeking species where they could gain the most nutritional benefits with the least energetic demands by selecting for species having both fruit and leaves available for consumption. Fruit consumed by these individuals included *Tamarindus indica*, a species that was also consumed for both its fruits and leaves by the other two individuals in this study. Because these data were only collected in the dry, winter months, it is possible that *Tamarindus indica* may act as a fallback food for the northern sportive lemur. Consuming *Tamarindus indica* as a fallback food source has been observed in other lemurs, especially for those living in disturbed areas during the dry months when overall food availability, especially fruit, is reduced (Sauther and Cuozzo 2009). Other species that were consumed by all individuals in both habitat types were *Leucaena leucocephala* and *Grewia triflora*, both of which were also fruiting at times during this study.

Although these data are preliminary, they suggest that the northern sportive lemur at Montagne des Français does slightly alter its diet in different forest patches. It appears that time budgets and overall plant species consumption did not vary between individuals. Those in areas with a greater number of different anthropogenic activities, however, spent more time consuming different food types, which could indicate dietary constraints. Alternatively, it is possible that the forest fragments were more similar than appeared from the data collected in this study. For example, the presence of more types of disturbances may not be as important as the severity of a single particular disturbance within a habitat. Additionally, because this species is a solitary forager, the overall level of anthropogenic disturbance in their habitat may not even be a constraining factor on their feeding ecology. A habitat with anthropogenic disturbance but that nonetheless contains some preferred species may be sufficient for a single individual to thrive.

Home range size has been reported for only four of the 26 species of sportive lemurs, but the estimated home ranges of 1.32−2.90 ha in the present study are larger than the 0.24−1.4 ha published ranges for other *Lepilemur* species (Hladik and Charles-Dominique 1974; Milton and May 1976; Warren and Crompton 1997; Zinner *et al*. 2003; Seiler 2012; Seiler *et al*. 2015). Our data show that individuals with a greater number of anthropogenic activities in their ranges and that consumed more fruit ('L' and 'M') have smaller and less distributed home ranges than the other individuals in this study ('F' and 'O'). This could indicate that although the activity budgets did not vary greatly between individuals, they may extend their home range in order to incorporate sufficient food sources, including a greater proportion of fruit, potentially compensating for a more altered environment. A similar response has been seen in *Eulemur* spp. and *Eulemur collaris* where populations living in human-altered degraded habitats had larger home ranges (Dehgan 2003; Schwitzer *et al*. 2011; Donati *et al*. 2011; Campera *et al*. 2014). It has also been suggested that long-tailed macaques (*Macaca fascicularis*) extended their home ranges in areas disturbed by drought and fire (Berenstain 1986). It is important to note that this pattern has been observed in frugivorous primates and has not been observed in other folivorous primates (Irwin 2008; Martinez 2008). More extensive data are needed to evaluate these potential factors and to determine if the northern sportive lemur does alter its behavior in other months of the year in response to varying degrees of anthropogenic activity.

It is important to note that the individual with the smallest estimated home range and lowest percentage of time consuming fruit ('L') was found in a habitat with the lowest

MBA, highest tree density, and second lowest TBA and diversity (H'), characteristics typically considered of more complex, degraded environments (Schwarzkopf and Rylands 1989; Grassi 2006). Similarly, individual 'O's habitat had the lowest TBA and diversity (H'), and a comparative MBA, also suggesting a complex, degraded environment, however, she spent a much greater percentage of time consuming fruit and had a larger home range than individual 'L'. This suggests that what appears to be a degraded habitat may not be driving individual northern sportive lemurs to alter their behavior at Montagne des Français. Instead, as previously noted variation in the lemurs' behavior could be due to the presence and degree of anthropogenic activities occurring within the home range, or alternatively, the spatial composition and abundance of significant feeding and sleeping trees within each individual home range.

The preliminary results obtained in this study are, at their most basic level, encouraging. Considering that the northern sportive lemur is currently living in different habitat fragments, at least from the behavioral and dietary comparisons quantified in this study, it seems that they are capable of adapting to the habitats with higher indicators of anthropogenic disturbances by incorporating more fruit into their diet and extending their range. Although our data show slight variations in behavior in different forest fragments, individuals are persisting and mating in varying degrees of degraded habitats at Montagne des Français. Previous studies have indicated that other folivorous primates, including lemurs, tend to have a more favorable response to forest disturbances and degradation than frugivores; certain lemur species may even increase their abundance, have more widespread and robust food resources, reduce their foraging time, and ultimately thrive in these types of environments (Irwin *et al*. 2010; Herrera 2011; Eppley *et al.* 2015, Sawyer *et al*. 2016). While it is unclear if the northern sportive lemur prefers degraded environments or intact forests, our data indicate that they are able to persist in various fragments within a degraded landscape. Nonetheless, the long-term conservation status of the northern sportive lemur is still of extreme concern. The limited distribution of this species is in direct conflict with the growing human population in the area and the easily accessible economic opportunities available to people within their habitat. Research suggests that once habitat fragmentation and degradation begin, the fragments continue to decrease in size and become less connected (Chatelain *et al.* 1996; Chapman *et al.* 2007; Tesfaye *et al.* 2013). This is of concern for the northern sportive lemur because other studies suggest that distance between trees and leaf quality are limiting constraints for *Lepilemur* spp. and they reach their limit in areas with moderate disturbance (Ganzhorn 1993). Furthermore, in cases of extreme fragmentation and isolation, native small mammal communities can disappear rapidly (Gibson *et al*. 2013). The deforestation and disturbance occurring at Montagne des Français is severe as poverty and dependence on non-timber forest products appears to be determining factors for the actions of local people.

Further studies and surveys involving the northern sportive lemur are needed in order to confirm the population size and broaden our knowledge of this Critically Endangered species. Additionally, long-term studies with a more robust sample size covering all seasons are needed in order to statistically determine if feeding ecology and home range size vary with type and frequency of anthropogenic activities. Additionally, by examining what tree species northern sportive lemurs prefer throughout the year will allow for the identification of more favorable habitats within Montagne des Français for subsequent conservation attention.

It is also imperative to evaluate the behavior of the local people and the driving forces behind their actions. Future work should identify the frequency and extent of the extraction of non-timber forest products (NTFP) by local populations. NTFPs, such as charcoal production, woodfuel, and bushmeat often support rural livelihoods as daily subsistence or supplemental income (Angelsen and Wunder 2003; Angelsen *et al*. 2014; Golden *et al.* 2014); however such a heavy reliance on NTFPs often has negative implications for the ecosystems providing these resources. Mapping the location of NTFP extraction in the area is essential in order to assess proximity to individual home ranges of northern sportive lemurs, and any associated behavioral changes. This can directly impact conservation initiatives and where selective logging may occur in the future. As habitat disturbance continues, the local people's willingness to actively participate in conservation measures (such as selective logging of only certain tree species), as well as the species' ability to withstand or adapt to these disturbances, will likely be determining factors in the persistence of northern sportive lemurs at Montagne des Français.

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