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Anthropogenic Disturbances and Deforestation of Northern Sportive Lemur (*Lepilemur septentrionalis*) Habitat at Montagne des Français, Madagascar

Mary P. Dinsmore[1,2], Karen B. Strier[3] and Edward E. Louis Jr.[4,5]

[1]*Nelson Institute for Environmental Studies, University of Wisconsin-Madison, Madison, WI, USA*
[2]*School of Environmental Sustainability, Loyola University Chicago, Chicago, IL, USA*
[3]*Anthropology Department, University of Wisconsin-Madison, Madison, WI, USA*
[4]*Center for Conservation and Research, Omaha's Henry Doorly Zoo and Aquarium,Omaha, NE, USA*
[5]*Madagascar Biodiversity Partnership, Antananarivo, Madagascar*

Abstract: Madagascar is experiencing some of the most persistent and alarming rates of anthropogenic forest loss, threatening its endemic flora and fauna. Numerous factors contribute to this forest degradation and loss, but in Madagascar it is most often attributed to heavy human reliance on forest products for income and survival. Montagne des Français (MDF) is a forest in northern Madagascar and the last remaining home of the Critically Endangered northern sportive lemur (*Lepilemur septentrionalis*). We assessed the type and frequency of anthropogenic disturbances observed at MDF, as well as the forest loss and fragmentation in this region over six decades. To assess current conditions, we systematically recorded occurrences of anthropogenic disturbances in ten lemur home ranges and three trails over two field seasons (June to July 2016; February to May 2017). To assess historical landcover change, we analyzed six, classified, 30-m resolution forest cover maps from 1953, 1973, 1990, 2000, 2010 and 2014. We recorded a total of 1,412 human-caused disturbances of eight different types in about 15 ha. Felled trees were the most frequently observed disturbance, with Bonaramatsigny (*Leucaena leucocephala*) the most frequently felled species. Forest cover at MDF drastically decreased from 76% in 1953, to 24% in 2014. Our results indicate that human disturbances are widespread and pervasive, contributing to overall forest cover loss and fragmentation at MDF, which impact the quality, connectivity, and availability of habitat for endemic lemurs of this region.

Key Words: Forest degradation, fragmentation, hunting, landcover change, logging, non-timber forest products

Introduction

Tropical forest systems are considered some of the most important ecological systems worldwide. They provide a suite of local and global ecosystem services including carbon storage, regulation of water quality and supply, climate control, and provisioning of food and materials to local people, and they support more species than any other ecosystem on Earth (Foley *et al*. 2007; Gibbs *et al*. 2007; Harper *et al*. 2007; Vieilledent *et al.* 2013). Thus, the immediate and long-term consequences of widespread tropical deforestation and degradation are immense.

Despite their ecological importance, tropical forests continue to be overexploited globally (Vitousek *et al.* 1997; Tilman *et al*. 2017; Seymour and Harris 2019). For many tropical countries (especially those in Asia and South America), the leading drivers of deforestation and degradation are large-scale agricultural expansion, commercial logging, and the growing demand for biofuels (Rudel *et al*. 2009; Gaspartos *et al*. 2011; Sayer *et al*. 2012). Deforestation in tropical Africa is still characterized, however, by the slow expansion of subsistence farming practices and the extraction of non-timber forest products (NTFP), such as fuelwood, charcoal, building materials, and food (Fisher 2010). The use of fuelwood, charcoal, and other NTFPs is prevalent throughout sub-Sahara Africa for fulfilling basic needs. Charcoal, for example, is the most widely used source of domestic energy for cooking in urban regions (Zulu and Richardson 2012; Ndegwa *et al.* 2016). In addition, charcoal production may aid in supporting rural livelihoods where they can act as safety-nets in times of uncertainty as well as supplement income and potentially provide a 'pathway out of poverty' (Angelsen and Wunder 2003; Angelsen *et al.* 2014).

The extent and pervasiveness of small-scale anthropogenic actions and NTFP extraction are the proximate drivers contributing to overall forest loss, degradation, and fragmentation in sub-Saharan Africa. Madagascar in particular is experiencing some of the most persistent and alarming rates of anthropogenic forest loss (Dewar and Richard 2012). Vieilledent *et al.* (2018) estimated that from 1953–2014 Madagascar lost 44% of its natural forest cover, with only 8.9 million ha of forest cover in 2014, and a rate of forest loss reaching 99,000 ha per year from 2010-2014 (1.08% per year). Specific areas of Madagascar have experienced even higher rates of forest loss, including the primary forest of Masoala, which showed increased rates from 2010–2011 (1.27% per year; Allnutt *et al*. 2013). The increased rate of forest loss may reflect the demands of Madagascar's growing population and the slow development of economic opportunities (Neudert *et al*. 2017). While the reliance on various forest products is widespread throughout Madagascar, fuelwood collection and charcoal production are predominant. Nearly 90% of Madagascar's population relies on biomass for their daily energy needs, resulting in approximately 18 million m^3 of wood being exploited for wood fuel yearly, half of which is converted to charcoal for use in urban areas (Meyers *et al*. 2006; Minten *et al*. 2012). Although the demand for forest products continues to grow in Madagascar, the country has seen an increase in the establishment of protected areas, resulting in tangible, if limited, effectiveness in reducing deforestation (Eklund *et al.* 2016; Gardner *et al*. 2018).

Such heavy extraction of NTFPs has significant implications for the ecosystems providing these resources. Fuelwood collection and charcoal production are the principal proximate drivers of forest degradation for African countries (Hosonuma *et al.* 2012). Habitat degradation reduces forest productivity, which leads to a suite of harmful effects for species living in these regions, including changes in habitat composition, loss of essential resources, edge effects, loss of potential to find mates, soil erosion, and increased vulnerability to hunters and poachers (Chapman and Lambert 2000; Lamb *et al.* 2005; Estrada *et al.* 2017). These deleterious consequences of forest degradation are of extreme concern for Madagascar, which is home to numerous endemic plants and animals, including 108 species of lemurs, 95% of which are today threatened with extinction (IUCN 2020; Schwitzer *et al.* 2014).

Anthropogenic disturbances pose two main threats to lemurs: (1) an immediate risk to their survival, and (2) alterations to habitat structure and quality (Michalski and Peres 2005; Godfrey and Irwin 2007; de Almeida-Rocha *et al*. 2017). Hunting results in the direct loss of populations and can inadvertently shift complex social systems and demographics. Logging, slash-and-burn agriculture, and cattle grazing alter forest spatial composition and quality, acting in similar ways to forest edges that tend to favor ruderal species (Tabarelli *et al.* 1999). Charcoal production is associated with biodiversity loss, especially when it is produced from slow-growing, hardwood species (Girard 2002; Naughton-Treves *et al*. 2007). It is generally understood that selective logging increases forest canopy gaps and reduces the proportion of larger trees (Johns 1997; Felton *et al*. 2003), changes that have severe implications for wildlife. In response to human-induced change, species may shift their behavior patterns concerning feeding, resting, and ranging (Strier 2009, 2017). Lemurs have been shown to reduce home range size, consumption of fruit, scent marking, traveling, and reproduction, and engage in fewer social interactions in disturbed forests in Madagascar (Irwin *et al*. 2010). Ultimately, species that are dependent on forests for dispersal will become more isolated as their inability to traverse matrix environments increases (Ricketts 2001), resulting in inbreeding depression and increased extinction risk (Simberloff and Cox 1987; Charlesworth and Charlesworth 1988; Couvet 2002).

Montagne des Français (henceforth MDF) is a fragmented forest in northern Madagascar, approximately 15 km southeast of the seaport town of Antsiranana. MDF is of ecological significance as it is the last remaining habitat of the Critically Endangered northern sportive lemur (*Lepilemur septentrionalis*; Louis *et al*. 2020), whose population is estimated to now be reduced to a mere 87 individuals (Bailey *et al.* 2020). Although several factors contribute to the overall population decline of this species, habitat loss and degradation are perhaps the most pervasive threats, as illegal logging, charcoal production, and sand extraction have been reported throughout MDF (Ranaivoarisoa *et al.* 2013).

Previously we have shown that different forests in MDF are affected by varying types of anthropogenic disturbances, such as tree felling, livestock grazing, and infrastructure development (Dinsmore *et al.* 2016); however, the extent and frequency of threats within individual lemur home ranges is unknown, as are their effects on overall deforestation and fragmentation within the greater MDF region. In this study we evaluate these uncertainties by assessing anthropogenic disturbances at MDF over two field seasons (June – August 2016 and February – May 2017) and analyzing historical and 30-m Landsat forest cover maps of MDF from 1953–2014. We predicted that, because of proximity to Antsiranana, a large urban region nearby, cut trees for fuelwood and/or charcoal production will be the most frequently observed human disturbance at MDF; and that forest loss per year will be greater at MDF than the overall rate of forest loss per year throughout Madagascar due to the extensive local reliance of forest products. We also predicted that overall forest loss will have been greatest between 1973 to 2000, the period after Madagascar's independence but before MDF became a protected zone in 2008, when there was some measure of enforcement and monitoring of illegal activity at MDF (Bailey *et al*. 2020).

Study Area

Our study was conducted at Montagne des Français in northern Madagascar (Fig. 1). This region is an isolated forest fragment of ~6500 ha that surrounds a calcareous massif at an elevation of 100–500 m (D'Cruze *et al*. 2007; Sabel *et al*. 2009; Ranaivoarisoa *et al*. 2013). MDF is characterized by two seasons: the wet months from December to April (average rainfall approximately 275 mm/month) and the dry, windy months from May to November (with winds reaching highs of 75 km/hr in June and July; Randrianarivelo *et al*. 2006). MDF was designated a protected zone in 2008 by the Service d'Appui à la Gestion de l'Environnement, making all cutting within the protected zone illegal, although instances of human use continue to be reported (Louis Jr. and Zaonarivelo 2015; Dinsmore *et al*. 2016). Proximity to the town of Antsiranana puts extreme pressure on the forests of MDF for charcoal, sand, and timber extraction. Consequently, the remaining forests of MDF are subject to erosion and fragmentation, reducing the vegetation to disturbed, secondary forest (D'Cruze *et a*l. 2007; Ranaivoarisoa *et al*. 2013). These disturbed fragments at MDF are the last remaining habitat of the Critically Endangered northern sportive lemur (Bailey *et al*. 2020). The Madagascar Biodiversity Partnership (MBP), a local NGO, established a field site at MDF (-12°20'02.4252", 049°21'32.4000") in 2012 to monitor northern sportive lemurs and aid in the reforestation and protection of the region.

Methods

Anthropogenic disturbances

To evaluate anthropogenic disturbances, in field season 1 (June to August 2016), the first author, Dinsmore, assisted by two MBP field guides, walked the entirety of locations where eight sportive lemurs had been observed in three sites that were known to local guides: (1) Vangisay, (2) Andranakomba, and (3) Ampamakiampafana. Three trails leading to the three forest sites were also surveyed to understand if human disturbances occurred on a wider scale outside of the official MDF protected area. This involved sampling 2.5 m on either side of the trail (Olupot *et al*. 2009; Naughton-Treves *et al*. 2011). The majority of the trails leading to the sites fell outside of the official protected zones in MDF. We understand that trails will show high levels of anthropogenic disturbances due to the ease of access to resources, but these data are essential to understand how resources are being used at various points throughout MDF. We chose to sample existing trails to each location as we did not want to create new transects in the highly sensitive protected zone. We walked the entirety of the habitat where sportive lemurs had been observed and recorded all visible disturbances rather than setting up sampling plots or transects, because the locations where the lemurs had been observed were small (about 1 ha). We defined human disturbance as any indication or trace of human presence or the use of forest

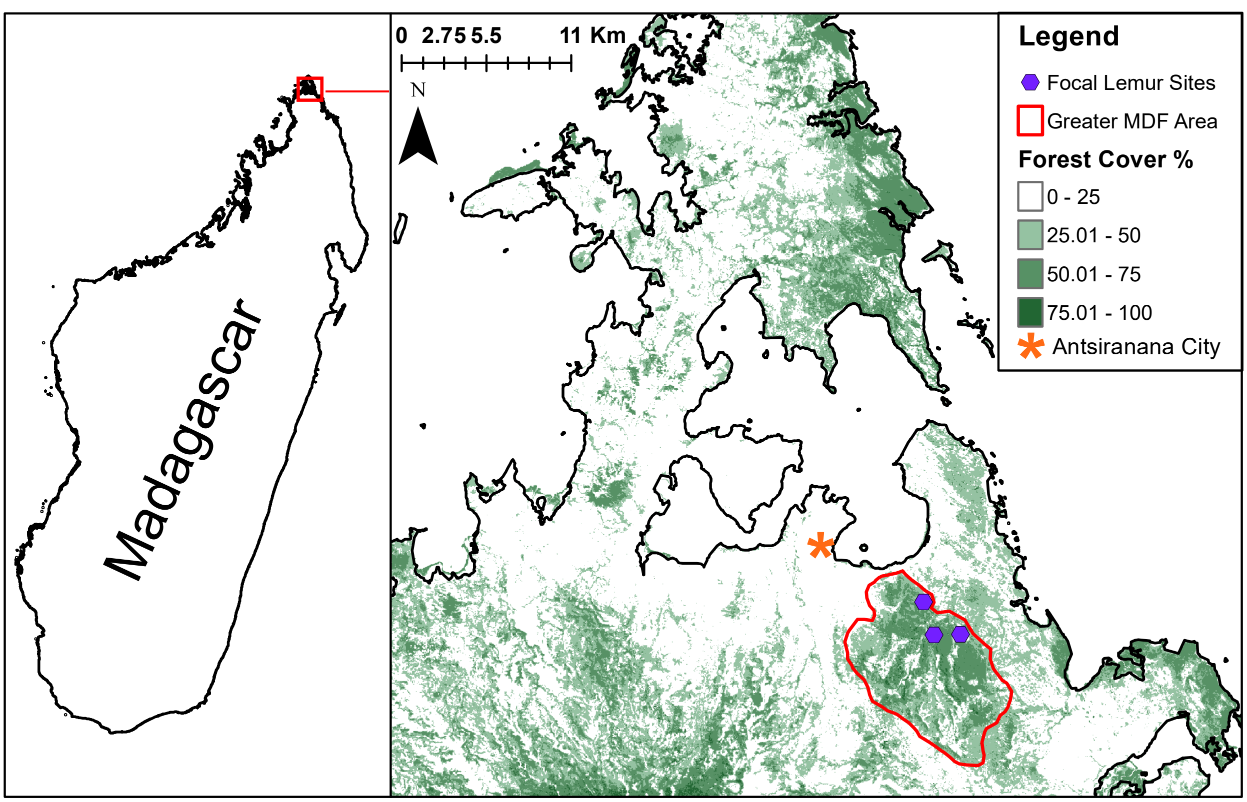

Figure 1. Location of study site, Montagne des Français, in northern Madagascar including the three focal forest sites of northern sportive lemurs and percent forest canopy cover. Percent of forest cover was retrieved from Hansen *et al*. (2013).

products by humans, which included but were not limited to: cut trees, presence or signs of zebu (local bovine), fire, human infrastructure, trash, or evidence of hunting (Olupot *et al.* 2009; Riley and Ellwanger 2013). We recorded every instance of human use and registered a GPS point at each location (Garmin GPSMap 64S). We additionally took note of the vernacular names of the cut tree species with the help of MBP field guides.

In field season 2 (February – May 2017), we resurveyed the same locations where the sportive lemurs had been observed as well as the trails to assess frequency of forest use. We walked each home range and trail, recording new visible signs, using the same methodology as in field season 1. To minimize chances of double counting, we only recorded newly felled logs, established traps, trash, and zebu dung. MBP guides assessed tree stumps and ax marks to determine how recently they had been felled. Two new focal individuals' (Pegasus, Dumbledore) home ranges were surveyed for the first time during the second field season (they were not resurveyed).

To assess if local populations targeted specific trees for felling at MDF, we established five, 20 m × 10 m plots in the habitat where individual lemurs had been observed at three different sites at MDF in June to July 2016 and February to May 2017. All trees >5.0 cm diameter at breast height in each plot were counted, and the vernacular name recorded, to get a representation of tree species composition at each site. We measured the felled tree selection ratio by dividing the percentage of felled tree species *i* by the percentage species *i* found in the plots and presumed to be available to those felling trees. A higher selection ratio value is indicative of a more preferred species while a selection ratio of 1 is indicative of a representative sample for the species' availability.

Behavioral Data

To understand how northern sportive lemurs use the habitat of MDF, Dinsmore, with the aid of two MBP guides, collected behavioral scans on nine lemurs (six females, three males) over the course of two field seasons. Individual northern sportive lemurs were followed for 2–3 consecutive days at a time. Instantaneous scan samples (Altmann 1974) were collected on focal individuals at 5-minute intervals for 5-6 hours or half-night follows (Ganzhorn *et al*. 2004; Dinsmore *et al.* 2016; Sawyer *et al*. 2017). Behaviors in our ethogram included: moving, feeding, resting, autogrooming, sleeping, drinking, defecating, urinating, and out of sight. For each scan, we recorded in which tree type the individual was located, and for feeding scans recorded the part and vernacular name of the food eaten by the focal individual. A GPS location point (Garmin GPSMAP 64S) was registered every 20 minutes to measure home range size.

Deforestation and Fragmentation

To assess landcover change at MDF we evaluated six, 30-m Landsat and historical forest cover maps from BiosceneMada spanning six decades: 1953, 1973, 1990, 2000, 2010, and 2014. The creation of these maps and the methodology are outlined by Vieilledent *et al.* (2018). We then digitalized a polygon of the greater MDF region by visual determination of the elevated masiff and surrounding forest using 15-m resolution TerraColor imagery, as no established geographic border of MDF is readily available. We clipped the polygon of MDF to each of the BiosceneMada forest cover maps in ArcMAP 10.7.1 to obtain forest cover of only MDF for all six years. These maps do not distinguish between various forest types (i.e. planted trees and agroforests versus traditional forest cover) and we made the assumption that all forested regions are suitable northern sportive lemur habitat.

Fragmentation was evaluated using FRAGSTATS 4.2 (McGariagal *et al*. 2012). For each yearly map, we analyzed three metrics to assess fragmentation: 1) total number of patches; 2) largest patch index; and 3) edge density. We evaluated the number of patches using the 4-neighbor rule, where two grid cells are considered a patch only if they share a flat adjacency, either horizontal or vertical (Pearson *et al*. 1996; Cardille and Turner 2017). We chose to use the 4-neighbor rule as a conservative analysis measure, as the species under study is a vertical clinger and leaper and does not easily traverse matrix environments. The largest patch index quantifies the percent of total landscape comprised by the largest patch, which acts as a rudimentary indicator of dominance in the landscape. Edge density calculates the total amount of edge in the landscape (m/ha).

Analysis

We assessed human-wildlife conflict by comparing the 12 trees most-used by the lemurs for feeding and moving through the forest with the most frequently felled trees by local people. Although we observed the sportive lemurs using vines for feeding and movement, vines were excluded from analysis because they were not targeted for felling. The vernacular names of the tree species were provided by trained, MBP guides. Dinsmore also collected and pressed plant samples in order to identify the Latin name for each species. They were examined and identified by staff of the Department of Botany at the Parc Botanique et Zoologique de Tsimbazaza in Antananarivo, Madagascar.

Individual lemur home ranges (ha) were calculated using UD kernel density estimates with the R-package, ADEhabitatHR (Calenge 2006). We chose to use a uniform smoothing parameter (Dinsmore *et al*. 2016; Wilmet *et al*. 2019) of h = 4.7, estimated by the LSCVh (least squares cross-validation) method (Dinsmore *et al.* 2016). We evaluated lemur home ranges at 95% contour, which gives the minimum area in which there is a 95% probability of finding the animal (Wilmet *et al*. 2019). We calculated trail length in m, multiplied it by 5 m (2.5 m on each side of trail), and then converted it to ha.

We established a threat index by calculating the total number of anthropogenic disturbances found in each lemur home range and trail and dividing it by its total size in order to determine a comparable number of threats/ha for each individual lemur and for each trail.

We calculated annual deforestation rate using the equation outlined by Vieilledent *et al*. (2018), which can be seen in Eq. (1). In this equation, Θ is the annual deforestation rate (in %/yr), and F_{t2} and F_{t1} correspond to the forest cover at dates t_2 and t_1, respectively. The time interval in years between the two dates is represented by t_2–t_1.

$$\theta = 100 \times [1 - (1 - \frac{F_{t2} - F_{t1}}{F_{t1}})^{(\frac{1}{t_2 - t_1})}]$$

Ethical Standards

The data were collected in accordance with Malagasy law, and the study granted under permits from the Ministère des Eaux et Forêts, numbers: 177/16/MEEF/SG/DSAP/SCB.Re (2016) and 21/17/MEEF/SG/DSAP/SCB.Re (2017). All our data were noninvasive and conducted under the University of Wisconsin – Madison's Animal Care Waiver for Observational Studies, granted on 27 February 2013. All focal northern sportive lemurs investigated in this study were wild caught and free-ranging, and capture was granted under permits to E. E. Louis Jr., 177/15/MEEF/SG/DGF/DSAP/SCB.Re (2016) and 24/17/MEEF/SG/DGF/DSAP/SCB.Re (2017). Focal lemurs were darted and immobilized in order to be fitted with radio telemetry collars. Individuals were darted with a CO^2 remote capture MJ Model DanInject rifle and PneuDarts using 10mg/ml of Telazol®. These darting methods and protocol follow those described in Louis *et al*. (2006). Collars were not removed after this study, as individual lemurs continue to be monitored by staff of the Madagascar Biodiversity Partnership.

Results

Anthropogenic disturbance

We recorded a total of 1,412 disturbances in approximately 15.15 ha at MDF over the two field seasons. We found 646 disturbances in 11.15 ha of individual lemur home ranges, while the nonoverlapping area that included the trails leading to each field site at MDF had 766 disturbances in about 3.99 ha. We observed eight types of disturbances: cut trees (including felled logs and tree stumps), charcoal pits, plantations (papaya), trash, zebu (both zebu feces and the zebus themselves), hunting (direct and indirect signs), infrastructure (such as the building of gates), and fire pits. Cut trees were the most observed disturbance, with a total of 1,268 felled trees. We observed a total of 97 different felled species at MDF, with the most frequently felled tree being Bonaramatsigny (*Leucaena leucocephala*; n = 181). Home ranges of individual lemurs varied from 0.63–2.58 ha, and the disturbance index ranged from 29–159 (threats/ha) for the lemur home range areas (Table 1). Disturbance indices were higher for the trails sampled leading to each of the three focal protected sites at MDF. Trail disturbance indices ranged from 141–224 threats/ha, and the number of threat types ranged from 4–7 (Table 1). Various types of disturbances observed at MDF are shown in Figure 2.

Both indirect and direct hunting were observed at MDF. We recorded five total instances, with three snares (presumed to be to trap tenrecs, family Tenrecidae), and on two occasions direct evidence of hunting: one instance of 11 tenrecs being carried out of the forest and a second in which lemurs were the target. On 25 March 2017, we found that the main sleep tree of Soavola (F), the only individual in Andrananakomba (site 2), had been cut down. The sleep

Table 1. Individual lemurs home range size, disturbance index and number of different threat types observed in each lemur home range and each trail leading to three different sites within Montagne des Français, Madagascar. Sex of individual is indicated as female (F) or male (M).

Lemur ID / Trail	Site	Home range or surveyed trail	Disturbance Index (threats/ha)	No of different threat types
Rozette (F)	1	0.77 ha	35	1
Marina (F)	1	1.17 ha	61	3
Vololana (F)	1	1.64 ha	103	4
Franqui (M)	1	2.58 ha	65	3
Soavola (F)	2	0.76 ha	159	3
Joanie (F)	3	0.63 ha	46	2
Pegasus (F)	3	0.63 ha	29	1
Fawkes (M)	3	0.82 ha	34	2
Karen (F)	3	0.77 ha	55	3
Dumbledore (M)	3	1.38 ha	52	2
Vangisay (Trail)	1	0.42 ha	143	4
Andrananakomba (Trail)	2	1.33 ha	151	7
Ampamakiampafana (Trail)	3	2.25 ha	224	6

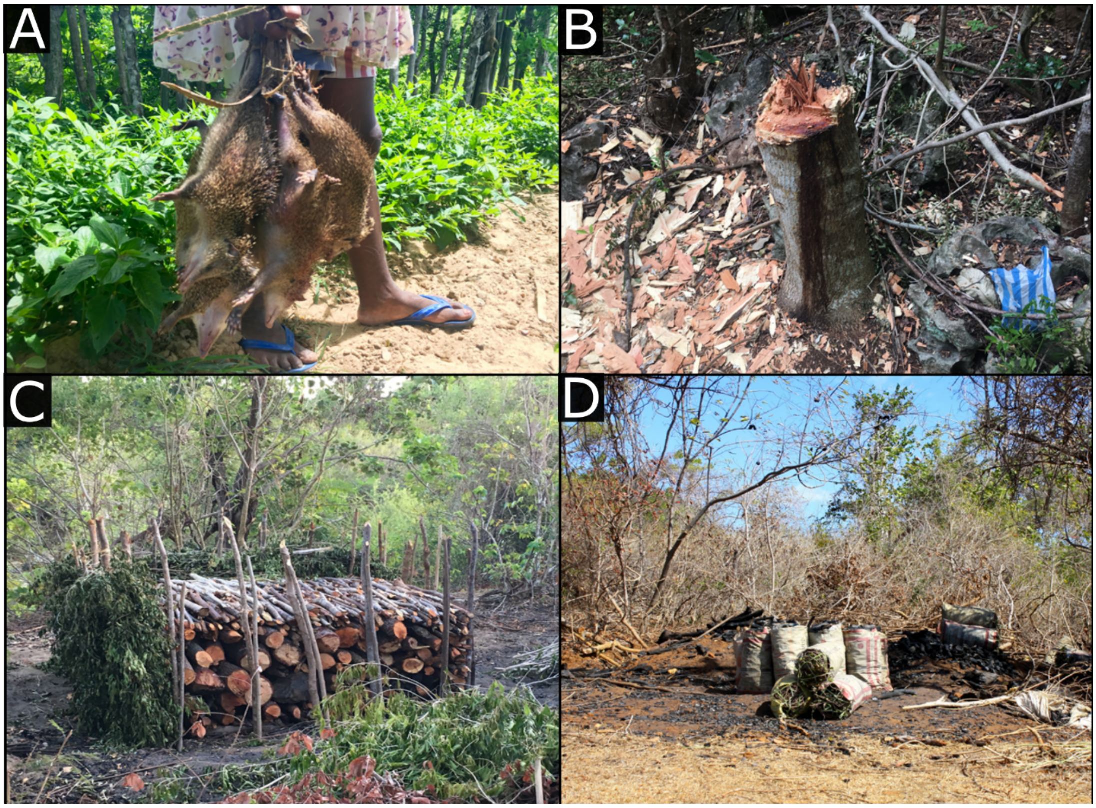

Figure 2. Various anthropogenic disturbances observed at Montagne des Français, Madagascar, during June to August 2016 and February to May 2017. Eight various types of disturbances were observed including: A) poaching of tenrecs (family Tenrecidae), B) recently cut tree and trash, C) charcoal heap, and D) bags of charcoal to be collected and sold in town.

hole had been cut into and her radio collar was hanging from the tree (Fig. 3).

Of the top 12 most felled trees at MDF, six were the sportive lemurs' most frequently used trees for feeding and travelling (Table 2). Madiromatsiko (*Tamarindus indica*) was the most used by sportive lemurs at MDF and was the 12th most felled tree. The tree felled most of all was Bonaramatsigny (*Leucaena leucocephala*), the 11th most used feeding tree species for the sportive lemurs. It was not a frequently used when travelling. Sely (*Grewia* spp.) was the second most felled tree at MDF, and the fourth most frequently in the lemurs's diet and second most used when moving around their home range. These findings suggest a considerable degree of human-lemur conflict.

The selection ratio of felled trees ranged from 0.5–50 (Table 2). Bonaramatsigny (*Leucaena leucocephala*), the most frequently felled tree, with a selection ratio of 4, suggesting that loggers targeted this species to some extent. Famoa (*Gagnebina commersoniana*) had the highest selection ratio of 50, suggesting that it was favored by loggers. Bonaramatsigny is infrequently used by northern sportive lemurs.

Deforestation and Fragmentation

The polygon established of MDF was 7,455 ha. In 1953, the maps showed MDF having 5,680.4 ha of forest, 76.2% coverage, but by 2014, our maps showed only 1,805.42 ha of forest, representing 24.2% total coverage (Table 3). Yearly rates of forest loss ranged from 0.5% to 3.2%, with the highest rates of yearly forest loss falling between 1973 and 1990 (Table 3). Visual representations of forest loss are depicted in Figure 4. From 1953 to 2000, the rates of yearly forest loss were higher at MDF than for Madagascar overall, including the dry forests (Table 3), but from 2000 to 2014, yearly rates of forest loss at MDF dropped, and were lower than those for all of Madagascar.

With the forest cover loss from 1953 to 2014, forest fragmentation at MDF also increased. The number of patches increased from 3 in 1953 to 151 in 2014 (Table 4). The largest-patch index and edge density also indicated a more fragmented landscape, with the largest patch index decreasing from 99.76% in 1953 to 20.98% in 2014, and edge density increasing from 10.91 m/ha to 159.05 m/ha over this same 60-year period (Table 4).

Discussion

Despite MDF being designated a protected area in 2008, our data indicate that anthropogenic disturbances are still widespread and ongoing. Disturbances were observed in every lemur home range and throughout the trail systems leading to each site. Anthropogenic disturbance indices were higher for the trail systems than in the lemur home ranges. We attribute this difference to the fact that trails provide easy access to areas from which to harvest and allow for easy removal of NTFPs (Mackenzie *et al*. 2012; Poor *et*

Table 2. Top 12 most observed felled tree species at Montagne des Français, Madagascar, from June-August 2016 and February-May 2017 and the top 12 most used feeding and travel trees of northern sportive lemurs (*Lepilemur septentrionalis*) during the same time period. Shaded tree species indicate those used by both humans and lemurs, suggesting possible human-wildlife conflict. Numbers of felled tree species indicate total counts of observed tree stumps or felled logs in ten lemur home ranges and three trails. The second number for felled tree species represents the selection ratio, an indicator of felled species preference. Numbers of feeding and travel trees indicate counts of times individual lemurs were observed feeding on or moving in each species. Vine species used by northern sportive lemurs for food or travel were not included in this analysis.

Top 12 felled tree species (and selection ratio)		Top 12 feeding trees of the northern sportive lemurs		Top 12 travelling trees of the northern sportive lemurs	
Bonaramatsigny *Leucaena leucocephala*	181 (4)	Madiromatsiko *Tamarindus indica*	168	Madiromatsiko *Tamarindus indica*	162
Sely *Grewia* spp.	134 (1)	Lonjo *Trilepisium madagascariense*	32	Sely *Grewia* spp	105
Magnary *Rourea orientalis*	107 (3)	Vahompy *Maytenus fasciculata*	28	Folerabonane *Delonix regia*	42
Taolanosy *Coptosperma* sp	74 (1)	Sely *Grewia* spp	26	Lonjo *Trilepisium madagascariense*	37
Famoa *Gagnebina commersoniana*	51 (50)	Manga *Mangifera indica*	23	Manga *Mangifera indica*	34
Vahompy *Maytenus fasciculata*	49 (1)	Bonarabe *Albizia lebbeck*	22	Vahompy *Maytenus fasciculata*	32
Somotroy *Fernandoa madagascariensis*	33 (1)	Taimpampango *Drypetes* sp.	18	Voankazomelako *Xanthocercis madagascariensis*	32
Madirokarana Species unknown	28 (11)	Adabu *Ficus polita*	15	Magnary *Rourea orientalis*	29
Lamoty *Ziziphus jujube*	27 (26)	Tsilaitry *Tina* sp.	15	Fagnamponga *Albizia polyphylla*	28
Sanaravatsy *Senna occidentalis*	26 (25)	Lamoty *Ziziphus jujube*	13	Bonarabe *Albizia lebbeck*	23
Somotsorana *Macphersonia gracile*	25 (1)	Bonaramatsigny *Leucaena leucocephala*	11	Vakakoana *Strychnos madagascariensis*	19
Madiromatsiko *Tamarindus indica*	22 (0.5)	Mandresy *Ficus trichopoda*	10	Tsilaitry *Tina* sp.	16

Table 3. Forest cover and deforestation rate for Montagne des Français, Madagascar, all forests of Madagascar (Vieilledent *et al*. 2018), and the dry forest of Madagascar (Vieilledent *et al*. 2018). Deforestation rates are denoted for the previous time periods to those listed (for example, 1973 rates are from 1953 to 1973, 1990 rates are for 1973 to 1990, etc.).

Year	MDF forest cover (ha)	MDF deforestation rate (%/year)	Madagascar forest cover (ha)	Madagascar deforestation rate (%/year)	Madagascar dry forest cover (ha)	Madagascar dry forest deforestation rate (%/year)
1953	5680	-	15,968,000	-	4,762,000	-
1973	4774	0.80	14,243,000	0.60	4,435,000	0.40
1990	2146	3.20	10,762,000	1.60	3,225,000	1.90
2000	1951	0.90	9,879,000	0.80	2,941,000	0.90
2010	1856	0.50	9,320,000	0.60	2,735,000	0.70
2014	1805	0.70	8,925,000	1.10	2,596,000	1.10

Table 4. Forest fragmentation of Montagne des Français, Madagascar from 1953 to 2014, as evaluated by total number of patches, largest patch index, and edge density.

Year	No. of patches (4-neighbor rule)	Largest Patch Index (%)	Edge density (m/ha)
1953	3	99.76	10.91
1973	32	88.78	60.97
1990	66	31.01	119.20
2000	62	23.47	117.09
2010	124	23.24	143.45
2014	151	20.98	159.05

al. 2019). Most of the trail systems sampled in this study also fall outside the officially protected zone of MDF (Fig. 5), decreasing possible encounters with local officials who may regulate the protected region. This, in turn, increases the likelihood for extraction of forest products at these unregulated locations.

Although every lemur home range experienced some degree of anthropogenic disturbance, higher and lower indices were associated with the various sites throughout MDF. Ampamakiampafana (site 3) had lower indices of human disturbance. This region is geographically farther from local villages and the larger seaport city of Antsiranana, making it

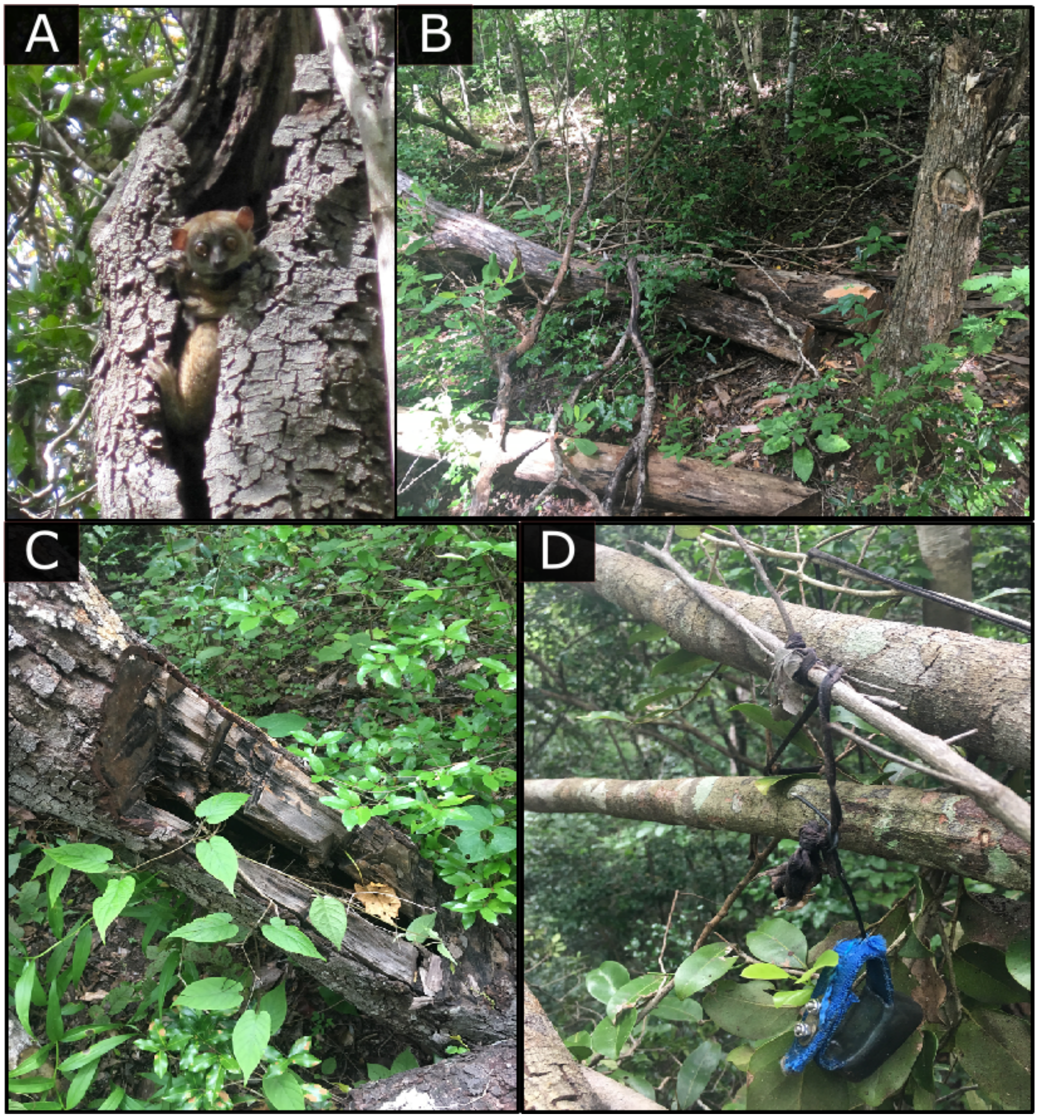

Figure 3. On 25 March 2017 the sleep tree of the only collared northern sportive lemur at Andrananakomba (site 2), Soavola (F), was found cut down. We presume this was an act of direct poaching. The various images depict: (A) Soavola resting in her known sleep tree, found directly on the path to Andrananakomba, (B) Cut sleep tree of Soavola, (C) Cut marks into her sleep hole within the tree, and (D) Radio collar of Soavola hung from cut sleep tree.

more difficult to reach and to extract forest products. Lemur home ranges at Vangisay (site 1) were experiencing moderate anthropogenic disturbance, which may be attributed to its closer proximity to local communities. However, it is also the closest site to two environmental nongovernmental organization (NGO) field camps. The presence of these NGOs may deter outside poachers and loggers from entering these forests (Campera *et al.* 2019). Andrananakomba (site 2) is approximately halfway between sites 1 and 3. We believe that this site served as a prime location for outsiders to extract NTFPs. Andrananakomba had the highest sampled home range of disturbance at MDF. Loggers were also observed harvesting trees on several occasions while we were collecting data. This site also was the only location where we observed hunting of northern sportive lemurs. While it is illegal to hunt lemurs in Madagascar, it has also been culturally taboo to engage in these types of actions (Jones *et al*. 2008). However, in more recent years, there has been a shift away from some traditional cultural norms as a result of widespread poverty and a stagnant economy, suggesting a possible growing demand and acceptance for the consumption of lemur bushmeat (Jenkins *et al*. 2011; Razafimanahaka *et al*. 2012; Borgerson *et al*. 2016; Merson *et al*. 2019). Populations with livelihoods that require extensive time in the forest may opportunistically hunt lemurs for their sustenance (Borgerson *et al*. 2016). Although we are unsure of the intent of the poachers at MDF, we suspect that loggers spent a lot of time at Andrananakomba, allowing for opportunistic hunting of lemurs there.

There was a high degree of overlap between trees preferentially used by lemurs and humans. Of the top 12 most frequently felled trees, six were used by sportive lemurs for feeding and traveling. Tamarind trees are the most frequently utilized feeding and traveling tree of NSLs, which was also the 12th most targeted tree by humans at MDF. Tamarind trees (*Tamarindus indica*) have widespread significance for both lemurs and humans throughout Madagascar. They are multipurpose resources for rural households, as they provide nutritional, medicinal, and cultural significance for communities; however, this species is also one of the most targeted species for felling for charcoal (Ranaivoson *et al*. 2015). The sportive lemurs feed on the leaves and fruit of tamarind trees in the dry and wet seasons (Dinsmore *et al*. 2016) indicating its importance as a staple resource for them. The most targeted tree by humans, *Leucaena leucocephala*, was the 11th most frequently used by the lemurs for feeding. While the conflict is not as great as some other trees, we believe that if local populations continue felling this species, it could reduce its numbers to the extent that it could become largely unavailable for the lemurs. Sely (*Grewia* spp.) is perhaps the tree with greatest conflict between northern sportive lemurs and humans at MDF. It was the second most harvested and the fourth most used by the lemurs for feeding and the second for traveling.

Anthropogenic use of NTFPs at MDF has greatly contributed to the deforestation and fragmentation of this landscape. There was a drastic decrease in overall forest cover at MDF from 76.2% in 1953 to 24.2% in 2014. There has been no reported industrialized agricultural or logging concessions at this location, suggesting that this increased

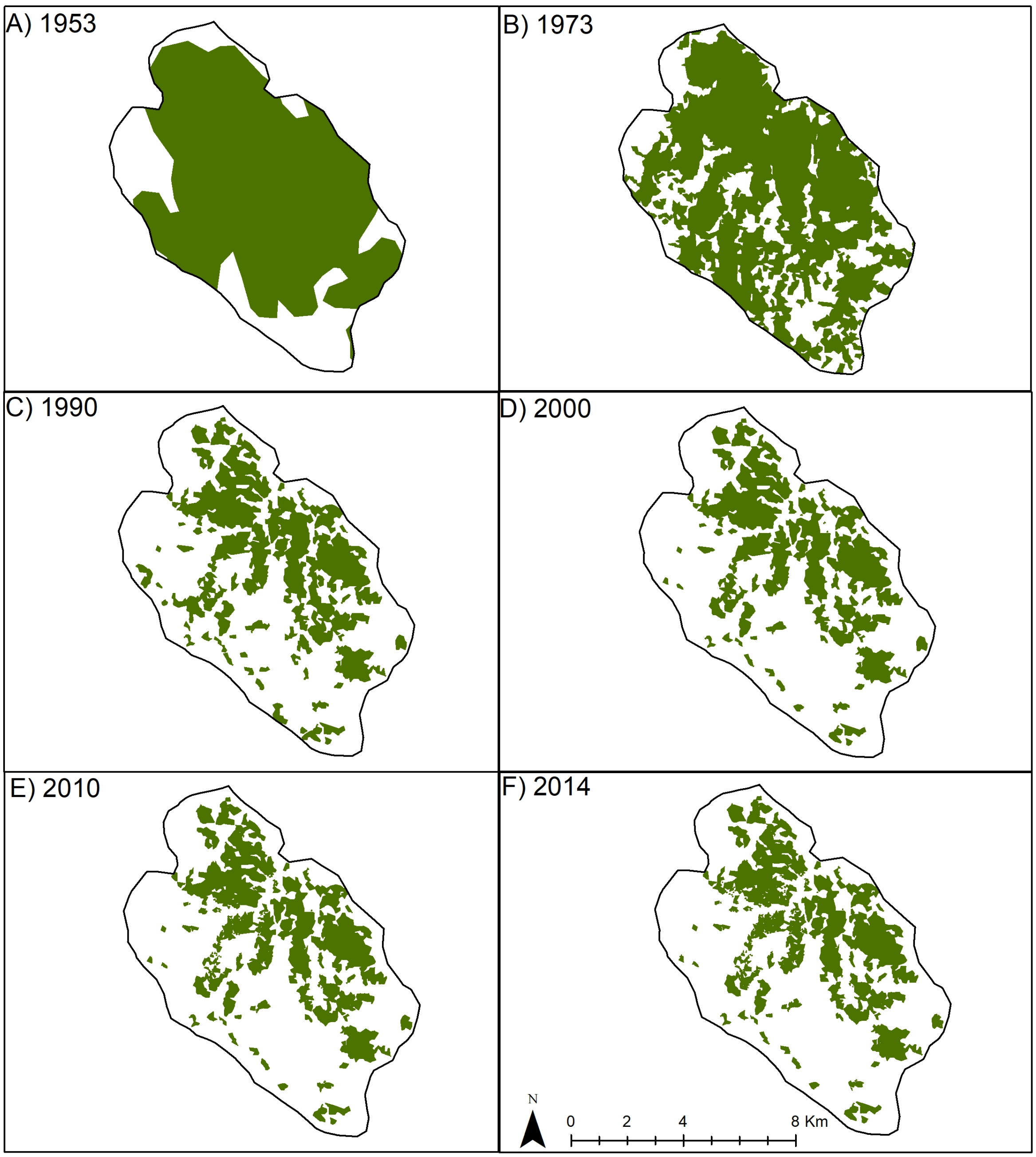

Figure 4. Maps of forest cover and fragmentation of Montagne des Français, Madagascar, spanning six decades. Forest cover for each year shows: A) 1953, 76.2%; B) 1973, 64.03%; C) 1990, 28.8%; D) 2000, 26.17%; E) 2010, 24.9%; and F) 2014, 24.22%.

deforestation and fragmentation is a result of long-term harvesting by local populations and individuals entering the area from the greater Antsiranana region. Rates of deforestation were higher at MDF than for all of Madagascar and for the dry forests of Madagascar from 1953 to 2000. Only after MDF was given protection in 2008 did the deforestation rate wane. The effectiveness of these protected zones depends, however, on local enforcement of the restrictions and regulations, the resource dependency of local populations, the growing size of the nearby city, and on stakeholder participation (Rasolofoson *et al*. 2015; Eklund *et al*. 2016; Waeber *et al*. 2016; Gardner *et al*. 2018). After 2000, there was overall less forest available at MDF from which to harvest. We believe that the increased fragmentation and forest loss from 1972 to 1990 made extraction of NTFPs more difficult, contributing to the slower rates of deforestation from 2000 to 2014.

The overall loss and fragmentation of forest habitat at MDF has greatly contributed to the decline in the population of the northern sportive lemur, today numbering around just 87 individuals at MDF (Bailey *et al*. 2020) and occurring nowhere else (Louis and Zaonarivelo 2015; Dinsmore *et al.* 2016). If we consider that the females have nonoverlapping home ranges, averaging 0.91 ha in size (Table 1) and the larger home ranges of the males overlap with those of females, then to sustain a population of at least three individuals (for example, 2 females and 1 male), a fragment would need to be at least 3 ha in size. Our data indicate that, in 2014, there were 1,805 ha of total forest cover divided among 151 fragments; however, there were only 1758 ha of forest in 41 fragments that were ≥3 ha.

The northern sportive lemur is considered to have a more generalist diet and can exploit a wide range of species (Dinsmore *et al*. 2016); however, over time, they may still

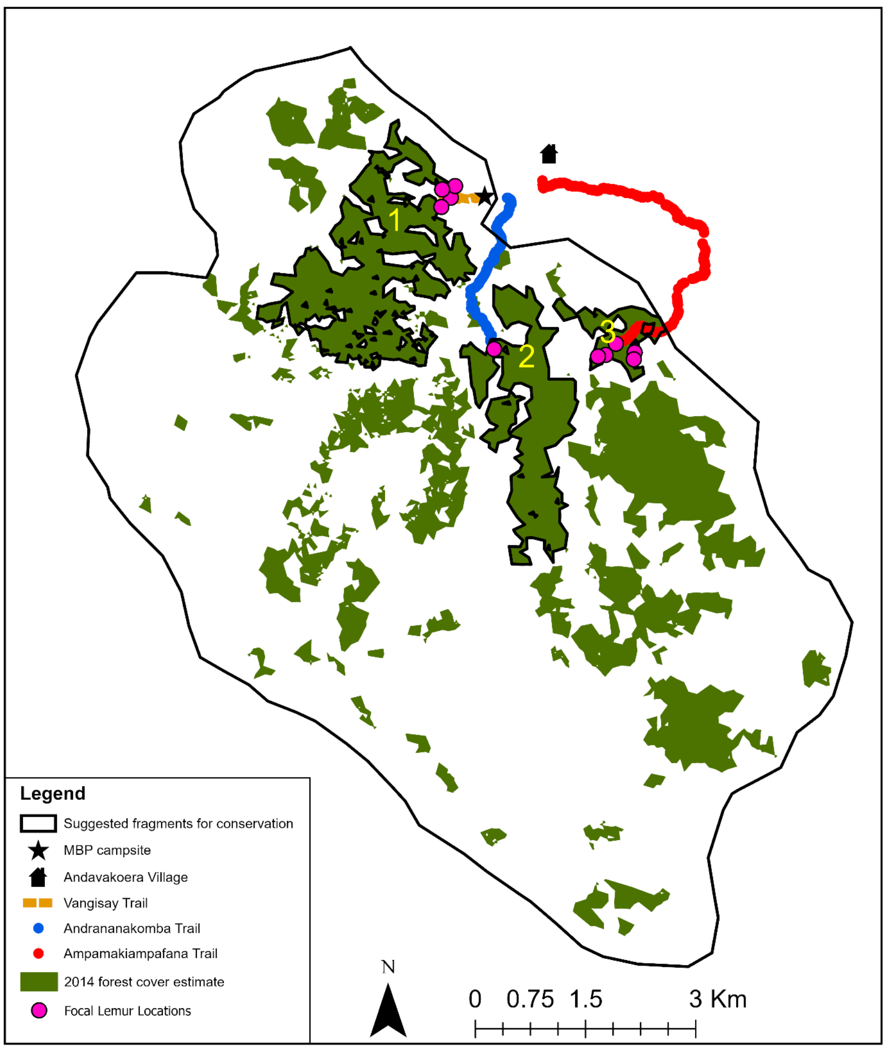

Figure 5. Fragments with known northern sportive lemurs (*Lepilemur septentrionalis*) are highlighted as conservation priority zones in Montagne des Français, Madagascar. Reforestation efforts should target connecting sites 1) Vangisay, 2) Andranankomba, and 3) Ampamakiampafana, as they are regions that are known to support sportive lemur populations and are some of the largest fragments that remain in MDF. The ten sampled individual lemur home range locations are represented within each of the three highlighted forest fragments.

be susceptible to human actions at MDF due to the overlap between the needs of lemurs and those of humans. The Madagascar Biodiversity Partnership (MBP) has worked with the regional Eaux et Forêt and gendarmerie (policing agency) to monitor and apprehend those extracting resources illegally. While the extent to which these patrols are aiding the lemurs is uncertain, it is promising that populations have increased from 50 to 87 known individuals (Bailey *et al*. 2020). We suggest that the MBP and other local environmental NGOs continue their efforts with the Eaux et Forêt and gendarmerie rangers to patrol this region, as well as work with local populations and perhaps campaign throughout the Antsiranana region to reduce the harvesting of the trees important for the lemurs at MDF. Unless alternative resources are made available, however, patrols will have limited lasting impact.

Sportive lemurs are vertical clingers and leapers and traversing open areas may prove difficult or even impossible. Some sportive lemurs have been shown to be limited by the distance between trees (Ganzhorn 1993). Our data indicate that the increased fragmentation coupled with dwindling habitat will limit the northern sportive lemur's ability to disperse to new forest habitats. Because they rely on arboreal locomotion, overall forest loss and fragmentation will inhibit them from dispersing to new territories, restricting gene flow in an already small population and potentially increasing intraspecific competition. We suggest that, for different reasons, the three patches, Vangisay (site 1), Andrananakomba (site 2), and Ampamakiampafana (site 3), should be conservation priority zones (Fig. 5), with initiatives to create forest corridors between them. Environmental NGOs, such as the Madagascar Biodiversity Partnership, are working with local communities to engage in reforestation efforts throughout MDF, and we propose that future reforestation efforts focus on the creation of habitat corridors between the three sites (Fig. 5), to increase gene flow and reduce potential inbreeding depression within this Critically Endangered species. The importance of connecting these sites is well illustrated considering the death of the last collared individual at site 2 (Andrananakomba), presumably poached on 25 March 2017 (Fig. 3). Recent surveys suggest that that these three locations still have sportive lemurs with moderate populations (Bailey *et al*. 2020), substantiating the need for connectivity for their dispersal.

Anthropogenic disturbance at MDF is directly impacting the northern sportive lemur through hunting, changing their habitat structure and composition through logging and cattle grazing, and directly impacting the population as forest fragmentation increases the isolation of remaining individuals. We predict that human reliance on NTFPs at MDF will continue to increase as Madagascar continues to battle extreme poverty and economic stagnancy. Continued conservation efforts by NGOs to reduce human-wildlife conflict and increase habitat connectivity will be essential for the persistence of the Critically Endangered northern sportive lemur in the Montagne des Français area.

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Literature Cited

Almeida-Richa, J. de, C. A. Peres and L. C. Oliveira. 2017. Primate responses to anthropogenic habitat disturbance: a pantropical meta-analysis. *Biol. Conserv.* 215: 30–38.

Allnutt, T. F., G. P. Asner, C. D. Golden and G. V. N. Powell. 2013. Mapping recent deforestation and forest disturbance in northeastern Madagascar. *Trop. Conserv. Sci.* 6: 1–15.

Altmann, J. 1974. Observational study of behavior: sampling methods. *Behaviour* 49, 227–267.

Angelsen, A., P. Jagger, R. Babigumira, B. Belcher, N. J. Hogarth, S. Bauch and S. Wunder, 2014. Environmental income and rural livelihoods: a global-comparative analysis. *World Develop.* 64, S12–S28

Angelsen, A. and S. Wunder. 2003. Exploring the forest-poverty link: key concepts, issues and research implications. *Center Intl. Forest. Res.* 40: 1–58.

Bailey, C. A., T. M. Sefczek, B. A. D. Robertson, L. Rasoamazava, V. F. Rakotomalala, J. D. N. Andriamadison, F. Randrianasolo, A. Andriajaona and E. E. Louis Jr. 2020. A re-evaluation of the northern sportive lemur (*Lepilemur septentrionalis*) population at Montagne des Français, and a review of its current state of conservation in the protected area. *Primate Conserv.* (34): 53–59.

Borgerson, C., M. A. McKean, M. R. Sutherland and L. R. Godfrey. 2016. Who hunts lemurs and why they hunt them. *Biol. Conserv.* 197: 124–130.

Calenge, C. 2006. The package "adehabitat" for the R software: a tool for the analysis of space and habitat use by animals. *Ecol. Model.* 197: 516–519.

Campera, M., M. Phelps, F. Besnard, M. Balestri, T. M. Eppley, V. Nijman and G. Donati. 2019. Does forest management and researchers' presence reducing hunting and forest exploitation by local communities in Tsitongambarika, south-east Madagascar? *Oryx* 53: 677–686.

Cardille, J. A. and M. G. Turner. 2017. Understanding landscape metrics. In: *Learning Landscape Ecology*, S. E. Gergel and M. G. Turner (eds.), pp.45–63. Springer, New York.

Charlesworth, D. and B. Charlesworth. 1987. Inbreeding depression and its evolutionary consequences. *Ann. Rev. Ecol. Syst.* 18: 237–268.

Chapman, C. A. and J. E. Lambert. 2000. Habitat alteration and the conservation of African primates: case study of Kibale National Park, Uganda. *Am. J. Primatol.* 50: 169–185.

Couvet, D. 2002. Deleterious effects of restricted gene flow in fragmented populations. *Conserv. Biol.* 16: 369–376.

D'Cruze, N., J. Sabel, K. Green, J. Dawson, C. Gardner, J. Robinson, G. Starkie, M. Vences and F. Glaw. 2007. The first comprehensive survey of amphibians and reptiles at Montagne des Français, Madagascar. *Herpetol. Conserv. Biol.* 2: 87–99.

Dewar, R. E. and A. F. Richard. 2012. Madagascar: A history of arrivals, what happened, and will happen next. *Ann. Rev. Anthropol.* 41: 495–517.

Dinsmore, M. P., E. E. Louis Jr, D. Randriamahazomanana, A. Hachim, J. R. Zaonarivelo and K. B. Strier. 2016. Variation in habitat and behavior of the northern sportive lemur (*Lepilemur septentrionalis*) at Montagne des Français, Madagascar. *Primate Conserv.* (30): 73–88.

Eklund, J., F. G. Blanchet, J. Nyman, R. Rocha, T. Virtanen and Cabeza, M. 2016. Contrasting spatial and temporal trends of protected area effectiveness in mitigating deforestation in Madagascar. *Biol. Conserv.* 203: 290–297.

Estrada, A. *et al.* 2017. Impending extinction crisis of the world's primates: Why primates matter. *Sci. Adv.* 3: 1–16.

Felton, A. M., L. M. Engström, A. Felton and C. D. Knott. 2003. Orangutan population density, forest structure and fruit availability in hand-logged and unlogged peat swamp forests in West Kalimantan, Indonesia. *Biol. Conserv.* 114: 91–101.

Fisher, B. 2010. African exception to drivers of deforestation. *Nature Geosci.* 3: 375–376.

Foley, J. A., G. P. Asner, M. H. Costa, M. T. Coe, R. DeFries, H. K. Gibbs, E. A. Howard, S. Olson, J. Patz, N. Ramankutty and P. Snyder. 2007. Amazonia revealed: forest degradation and loss of ecosystem goods and services in the Amazon Basin. *Front. Ecol. Environ.* 5: 25–32.

Ganzhorn, J. U. 1993. Flexibility and constraints of *Lepilemur* ecology. In: *Lemur Social Systems and Their Ecological Basis*, P. M. Kappeler and J. U. Ganzhorn (eds.), pp.153–165. Plenum Press, New York.

Ganzhorn, J. U., T. Pietsch, J. Fietz, S. Gross, J. Schmid and N. Steiner. 2004. Selection of food and ranging behaviour in a sexually monomorphic folivorous lemur*: Lepilemur ruficaudatus*. *J. Zool., Lond.* 263: 393–399.

Gaspartos, A., P. Stromberg and K. Takeuchi. 2011. Biofuels, ecosystem services and human wellbeing: putting biofuels in the ecosystem services narrative. *Agric. Ecosyst. Environ.* 142: 111–128.

Gardner, C. J., M. E. Nicoll, C. Birkinshaw, A. Harris, R. E. Lewis, D. Rakotomalala and A. N. Ratsifandrihamanana. 2018. The rapid expansion of Madagascar's protected area system. *Biol. Conserv.* 220: 29–36.

Gibbs, H. K., S. Brown, J. O. Niles and J. A. Foley. 2007. Monitoring and estimating tropical forest carbon stocks: making REDD a reality. *Environ. Res. Lett.* 2: 045023.

Girard, P. 2002. Charcoal production and use in Africa: what future? *Unasylva* 53: 30–35.

Godfrey, L. R. and M. T. Irwin. 2007. The evolution of extinction risk: past and present anthropogenic impacts on the primate communities of Madagascar. *Folia Primatol.* 78: 405–419.

Harper, G. J., M. K. Steininger, C. J. Tucker, D. Juhn and F. Hawkins. 2007. Fifty years of deforestation and forest fragmentation in Madagascar. *Environ. Conserv.* 54: 325–333.

Hosonuma, N., M. Herold, V. De Sy, R. S. De Fries, M. Brockhaus, L. Verchot, A. Angelsen and E. Romijn. 2012. An assessment of deforestation and forest degradation drivers in developing countries. *Environ. Res. Lett.* 7: 044009.

Irwin, M. T. *et al.* 2010. Patterns of species change in anthropogenically disturbed forests of Madagascar. *Biol. Conserv.* 143: 2351–2362.

IUCN. 2020. Almost a third of lemurs now critically endangered. IUCN Red List. URL: <https://www.iucn.org/news/species/202007/almost-a-third-lemurs-and-north-atlantic-right-whale-now-critically-endangered-iucn-red-list>.

Jenkins, R. K. B., A. Keane, A. R. Rakotoarivelo, V. Rakotomboavonjy, F. H. Randrianandrianina, H. J. Razafimanahaka, S. R. Ralaiarimamala and J. P. G. Jones. 2011. Analysis of patterns of bushmeat consumption reveals extensive exploitation of protected species in eastern Madagascar. *PLoS One* 6: e27570.

Johns, A. G. 1997. *Timber Production and Biodiversity Conservation in Tropical Rain Forests.* Cambridge University Press, Cambridge, UK.

Jones, J. P. G., M. M. Andriamarovololona and N. Hockley. 2008. The importance of taboos and social norms to conservation in Madagascar. *Conserv. Biol.* 22: 976–986.

Lamb, D., P. D. Erskine and J. A. Parrotta. 2005. Restoration of degraded tropical forest landscapes. *Science* 310: 1628–1632.

Louis Jr, E. E., C. A. Bailey, C. L. Frasier, T. M. Sefczek, B. Raharivololona, C. Schwitzer, J. Ratsimbazafy, L. Wilmet, A. Andriajaona, L. Rasoamazava, V. F. Rakotomalala and M. Dinsmore. 2020. *Lepilemur septentrionalis*. The IUCN Red List of Threatened Species 2020: e.T11622A115567059.

Louis Jr, E. E. and J. R. Zaonarivelo. 2015. Northern Sportive Lemur. In: *Primates in Peril: The World's 25 Most Endangered Primates 2014–2016*, C. Schwitzer, R. A. Mittermeier, A. B. Rylands, F. Chiozza, E. A. Williamson, J. Wallis and A. Cotton (eds.), pp.36–37. IUCN SSC Primate Specialist Group, International Primatological Society, Conservation International, and Bristol Zoological Society, Arlington, VA.

Mackenzie, C. A., C. A. Chapman and R. Sengupta. 2012. Spatial patterns of illegal resource extraction in Kibale National Park, Uganda. *Environ. Conserv.* 39: 38–50.

McGarigal, K., S. A. Cushman and E. Ene. 2012. FRAGSTATS v4: Spatial Pattern Analysis Program for Categorical and Continuous Maps. Computer software program produced by the authors at the University of Massachusetts, Amherst. URL: <http://www.umass.edu/landeco/research/fragstats/fragstats.html>.

Merson, S. D., L. J. Dollar, P. J. Johnson and D. W. Macdonald. 2019. Poverty not taste drives the consumption of protected species in Madagascar. *Biodiv. Conserv.* 28: 3669–3689.

Michalski, F. and C. A. Peres. 2005. Anthropogenic determinants of primate and carnivore local extinctions in a fragmented forest landscape of southern Amazonia. *Biol. Conserv.* 124: 383–396.

Minten, B., K. Sander and D. Stifel. 2012. Forest management and economic rents: Evidence from the charcoal trade in Madagascar. *Energy Sustain. Dev.* 116: 106–115.

Meyers D, B. S. Ramamonjisoa, J. Sève, M. Rajafindramanga and C. Burren. 2006. *Etude sur la consommation et la production en produits ligneux a Madagascar. Projet d'appui à la gestion durable de l'environnement et des écosystèmes forestiers à Madagascar.* Projet Jariala, USAID, 87. 34pp.

Naughton-Treves, L., D. M. Kammen and C. Chapman. 2007. Burning biodiversity: woody biomass use by commercial and subsistence groups in western Uganda. *Biol. Conserv.* 134: 232–241.

Naughton-Treves, L., J. Alix-Garcia and C. A. Chapman. 2011. Lessons about parks and poverty from a decade of forest loss and economic growth around Kibale National Park, Uganda. *Proc. Natl. Acad. Sci. U.S.A.* 108: 13919–13924.

Neudert, R., J. U. Ganzhorn and F. Wätzold. 2017. Global benefits and local costs—the dilemma of tropical forest conservation: a review of the situation in Madagascar. *Environ. Conserv.* 44: 82–96.

Ndegwa, G., D. Anhuf, U. Nehren, A. Ghilardi and M. Iiyama. 2016. Charcoal contribution to wealth accumulation at different scales of production among the rural population of Mutomo District in Kenya. *Energy Sustain. Dev.* 33: 167–175.

Olupot, W., R. Barigyira and C. A. Chapman. 2009. The status of anthropogenic threat at the people-park interface of Bwindi Impenetrable National Park, Uganda. *Environ. Conserv.* 36: 41–50.

Pearson, S. M., M. G. Turner, R. H. Gardner and R. V. O'Neill. 1996. An organism-based perspective of habitat fragmentation. In: *Biodiversity in Managed Landscapes: Theory and Practice*, R. C. Szaro and D. W. Johnston (eds.), pp.77–95. Cambridge University Press, New York.

Poor, E. E., V. I. M. Jati, M. A. Imron and M. J. Kelly. 2019. The road to deforestation: edge effects in an endemic ecosystem in Sumatra, Indonesia. *PLoS One* 14: e0217540.

Rasolofoson, R. A., P. J. Ferraro, C. N. Jenkins and J. P. G. Jones. 2015. Effectiveness of community forest management at reducing deforestation in Madagascar. *Biol. Conserv.* 184: 271–277.

Ranaivoarisoa, J. F., J. Zaonarivelo, L. Runhua, S. E. Johnson, T. Wyman, R. A. Mittermeier and E. E. Louis Jr. 2013. Rapid survey and assessment of the northern sportive lemur, *Lepilemur septentrionalis*, in northern Madagascar. *Primate Conserv.* (27): 23–31.

Ranaivoson, T., K. Brinnkmann, B. Rakouth and A. Buerkert. 2015. Distribution, biomass and local importance of tamarind trees in south-western Madagascar. *Global Ecol. Conserv.* 4 : 14–25.

Randrianarivelo, C., C. Birkinshaw, J. Raharimampionona, S. Andriambololonera, O. Randriambololomamonjy, T. Rabefarihy, L. Randrianaina, L. Randrianaina, A. Ravoahangy, R. Razafindrasoa, A. Tianarifidy and S. Serge. 2006. Montagne des Français: Description evaluation et strategie de conservation. Report, Missouri Botanical Garden, St Louis, MO.

Razafimanahaka, J. H., R. K. B. Jenkins, D. Andriafidison, F. Randrianandrianina, V. Rakotomboavonjy, A. Keane and J. P. Jones. 2012. Novel approach for quantifying illegal bushmeat consumption reveals high consumption of protected species in Madagascar. *Oryx*, 46, 584–592.

Ricketts, T. H. 2001. The matrix matters: effective isolation in fragmented landscapes. *Am. Nat.* 158: 87–99.

Riley, E. P. and A. L. Ellwanger. 2013. Methods in ethnoprimatology: exploring the human- non-human primate interface. In: *Primate Ecology and Conservation: A Handbook of Techniques*, E. Sterling, N. Bynum and M. Blair (eds.), pp.128–150. Oxford University Press, Oxford, UK.

Rudel, T. K., R. Defries, G. P. Asner and W. F. Laurance. 2009. Changing drivers of deforestation and new opportunities for conservation. *Conserv. Biol.* 23: 1396–1405.

Sabel, J., K. Green, J. Dawson, J. Robinson, C. Gardner, G. Starkie and N. D'Cruze. 2009. The conservation status of mammals and avifauna in the Montagne des Français massif, Madagascar. *Madagascar Conserv. Dev.* 4: 44–51.

Sawyer, R. M., Z. S. E. Fenosoa, A. Andrianarimisa and G. Donati. 2017. The effect of habitat disturbance on the abundance of nocturnal lemur species on the Masoala Peninsula, northeastern Madagascar. *Primates* 58: 187–197.

Sayer, J., J. Ghazoul, P. Nelson and A. K. Boedhihartono. 2012. Oil palm expansion transforms tropical landscapes and livelihoods. *Glob. Food Sec.* 1: 114–119.

Schwitzer, C. *et al.* 2014. Averting lemur extinction amid Madagascar's political crisis. *Science* 343: 842–843.

Simberloff, D. and J. Cox. 1987. Consequences and costs of conservation corridors. *Conserv. Biol.* 1: 63–71.

Seymour, F. and N. L. Harris. 2019. Reducing tropical deforestation. *Science* 365: 756–757.

Strier, K. B. 2009. Seeing the forest through the seeds: mechanisms of primate behavioral diversity from individuals to populations and beyond. *Curr. Anthropol.* 50: 213–228.

Strier, K. B. 2017. What does variation in primate behavior mean? *Am. J. Phys. Anthropol.* 162: 4–14.

Tabarelli, M., W. Mantovani and C. A. Peres. 1999. Effects of habitat fragmentation on plant guild structure in the montane Atlantic forest of southeastern Brazil. *Biol. Conserv.* 91: 119–127.

Tilman, D., M. Clark, D. R. Williams, K. Kimmel, S. Polasky and C. Packer. 2017. Future threats to biodiversity and pathways to their prevention. *Nature* 546: 73–81.

Vieilledent, G., C. Grinand and R. Vaudry. 2013. Forecasting deforestation and carbon emissions in tropical developing countries facing demographic expansion: a case study in Madagascar. *Ecol. Evol.* 3: 1702–1716.

Vieilledent, G., C. Grinand, F. A. Rakotomalala, R. Ranaivosoa, J. R. Rakotoarijaona, T. F. Allnutt and F. Achard. 2017. Combining global tree cover loss data with historical national forest-cover maps to look at six decades of deforestation and forest fragmentation in Madagascar. *Biol. Conserv.* 222: 189–197.

Vitousek, P. M., H. A. Mooney, J. Lubchenco and J. M. Melillo. 1997. Human domination of Earth's ecosystems. *Science* 277: 494–499.

Waeber, P. O., L. Wilmé, J.-R. Mercier, C. Camara and P. P. Lowry II. 2016. How effective have thirty years of internationally driven conservation and development efforts been in Madagascar? *PLoS One* 11: e0161115.

Wilmet, L., R. C. Beudels-Jamar, C. Schwitzer, H. Rakotondrainibe, P. Devillers and C. Vermeulen. 2019. Use of space and home range characteristics of *Lepilemur mittermeieri*, an endangered sportive lemur endemic to the Ampasindava peninsula, north-west Madagascar. *Am. J. Primatol.* 81: e23017.

Zulu, L. C. and R. B. Richardson. 2013. Charcoal, livelihoods, and poverty reduction: evidence from Sub-Saharan Africa. *Energy Sustain. Dev.* 17: 127–137.

Authors' addresses:
Mary P. Dinsmore, School of Environmental Sustainability, Loyola University Chicago, Chicago IL, 60660; **Karen B. Strier**, Anthropology Department, University of Wisconsin-Madison, Madison WI, USA; and **Edward E. Louis Jr.**, Center for Conservation and Research, Omaha's Henry Doorly Zoo and Aquarium, Omaha, NE, USA.

Corresponding author: Mary P. Dinsmore
email: <mdinsmore@luc.edu>.

Mary P. Dinsmore ORCID iD: https://orcid.org/0000-0002-0146-8399
Karen B. Strier ORCID iD: https://orcid.org/0000-0003-25 20-9110
Edward E. Louis Jr. ORICID iD: https://orcid.org/0000-0002 -3634-4943

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