



Ecological Correlates to Lemur Community Structure in Southeast Madagascar

Shawn M. Lehman,^{1,4} Jonah Ratsimbazafy,² Andry Rajaonson,³
and Sabine Day³

Received March 8, 2005; revision July 6, 2005; accepted August 14, 2005;

Published Online September 8, 2006

The Fandriana-Marolambo forest corridor is one of the largest (ca. 250,000 ha) and least explored tracts of unprotected forest in southeast Madagascar. Although published range maps show continuous distributions for many lemurs throughout the region, there are few data on lemur community structure in the corridor. We aimed to determine lemur community structure, with its ecological correlates (altitude, agriculture, selective logging, and hunting), in the Fandriana-Marolambo forest corridor. We surveyed 7 sites and sighted 4 nocturnal taxa (Avahi laniger, Cheirogaleus major, Lepilemur mustelinus, and Microcebus rufus) and 6 diurnal taxa (Eulemur rubriventer, E. fulvus rufus, E. f. fulvus, Propithecus diadema edwardsi, Hapalemur griseus griseus, and Varecia variegata variegata). Composition of the lemur community was broadly similar to that of nearby protected areas (Ranomafana and Mantadia National Parks). However, we sighted no Hapalemur aureus, H. simus, or Indri indri, and observed Propithecus diadema edwardsi and Varecia variegata variegata at only 1 site each. We sighted an apparent hybrid form of Eulemur fulvus fulvus and E. f. rufus that may represent a new hybrid zone for lemurs. After testing for spatial autocorrelation, lemur diversity correlates negatively with altitude and agricultural intensity. Though the Government of Madagascar is assessing the corridor as a new national park, we suggest conservation

¹Department of Anthropology, University of Toronto, Toronto, Ontario M5S 3G3, Canada.

²Durrell Wildlife Conservation Trust, Antananarivo, Madagascar.

³Department of Paleontology, University of Antananarivo, Antananarivo, Madagascar.

⁴To whom correspondence should be addressed; e-mail: slehman@chass.utoronto.ca.

plans for local lemurs are complicated by population isolation and lack of data on minimum viable size of the proposed protected area.

KEY WORDS: community structure; conservation; deforestation; hunting; lemurs.

INTRODUCTION

Lemurs are among the world's highest conservation priorities (Brummitt and Lughadha, 2003; Ganzhorn *et al.*, 2001; Sechrest *et al.*, 2002) because they are endemic to Madagascar and many taxa require conservation attention (Ganzhorn *et al.*, 2001; Goodman and Benstead, 2005; Lehman, 2006). For example, of the approximately 52 lemur taxa, 33% ($N=17$) are endangered or critically endangered (IUCN, 2004). Moreover, only 10–20% of the original forest cover remains in Madagascar (Du Puy and Moat, 1996, 1998; Green and Sussman, 1990). Deforestation occurs mainly as the result of slash-and-burn agriculture, known locally as tavy, and selective logging by local people. Hunting of lemurs is prevalent, including in protected areas (Goodman and Raselimanana, 2003; Lehman and Wright, 2000; Mutschler *et al.*, 2001), resulting in considerable efforts to determine conservation priorities for lemurs (ANGAP, 2003; Ganzhorn *et al.*, 1996/1997, 1997, 2001; G.E.F., 1996a, b). Hannah *et al.* (1998) and Ganzhorn *et al.* (1997) described results of a multidisciplinary conference to assess Madagascar's scientific and conservation priorities. The participants concluded that an urgent need exists for biological research outside protected areas in Madagascar.

The Fandriana-Marolambo forest corridor is one of the largest (*ca.* 250,000 ha) and least explored tracts of unprotected forest in SE Madagascar (Fig. 1). Short-term surveys at sites near the corridor found agriculture, selective logging, and hunting create intense pressure for lemurs (Irwin *et al.*, 2000; Lehman and Wright, 2000). The potential loss of lemur populations is alarming because range maps based largely on subjective impressions of lemur biogeography show continuous distributions for many species throughout the corridor (Garbut, 1999; Mittermeier *et al.*, 1992, 1994; Rowe, 1996; Wolfheim, 1983). For example, the maps tend to show 2 endangered lemurs, Milne-Edward's sifakas (*Propithecus diadema edwardsi*) and black-and-white ruffed lemurs (*Varecia variegata variegata*), as ranging throughout the Fandriana-Marolambo forest corridor.

If intersite differences in lemur community structure exist in the corridor, then it is important to determine if the variation correlates with natural or anthropogenic factors or both. The distinction is important because naturally occurring factors, such as altitude, can erroneously lead researchers and conservation authorities to conclude that lemur extirpations are caused by human activities. Altitude and associated habitat variations can prevent

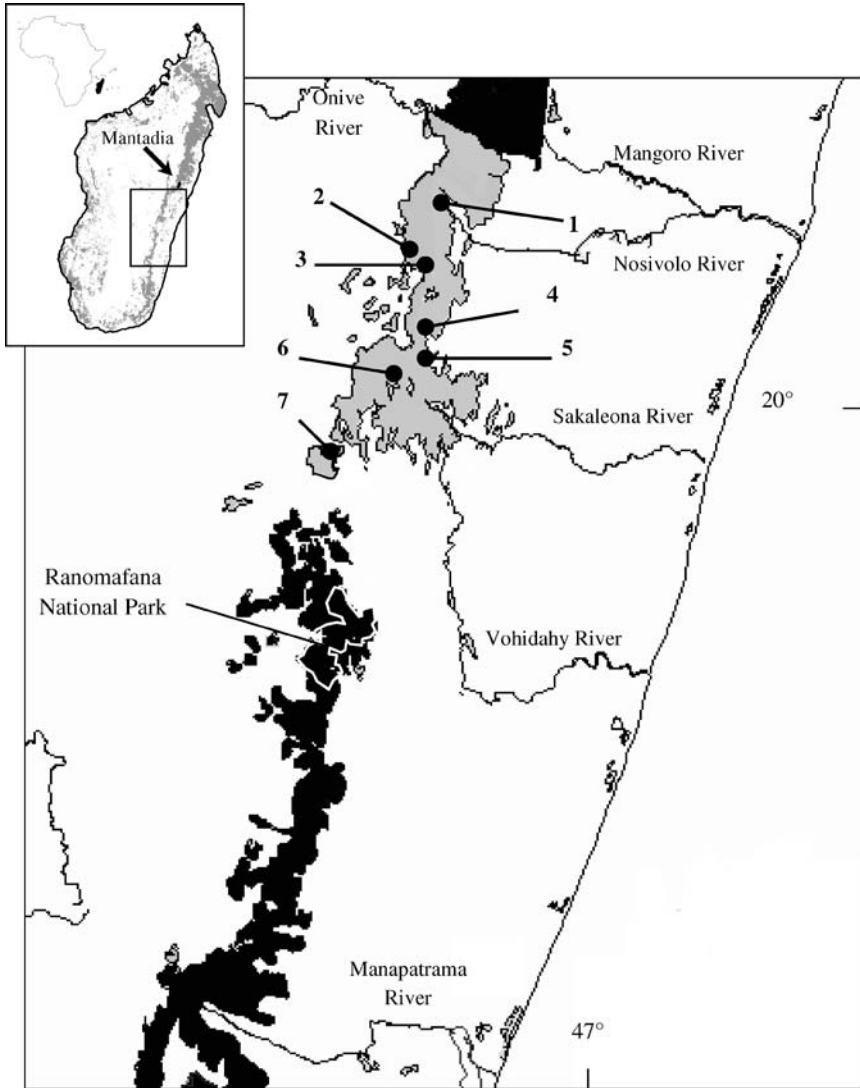


Fig. 1. Location of 7 survey sites in the Fandriana-Marolambo forest corridor (numbers refer to sites described in Table I) as well as nearby protected areas (Ranomafana and Mantadia National Parks). Gray areas refer to the Fandriana-Marolambo forest corridor. Black areas refer to other forest habitats in SE Madagascar.

some lemur taxa from living at high-altitude sites in the corridor (Goodman and Ganzhorn, 2003). Conversely, agriculture, selective logging, and hunting influence the community structure of plants and animals in Madagascar (Ganzhorn and Schmid, 1998; Harcourt and Parks, 2003; Vallan, 2002).

We report on variations in lemur community structure in the Fandriana-Marolambo forest corridor, with a focus on answering: (1) What is the structure of the lemur community in the corridor? and (2) Is lemur diversity correlated with altitude or anthropogenic disturbances (deforestation, hunting), or both?

METHODS

The Fandriana-Marolambo forest corridor is located in SE Madagascar, between 20° 0'S and 47° 39'E (Fig. 1). Vegetation in the corridor comprises grasslands, agricultural fields, and forest fragments of varying shapes and sizes. Intensive cultivation of lands surrounding forests in the corridor occurs, as in many areas in SE Madagascar. Cultivation involves rice paddies and agricultural crops such as sugar cane (*Saccharum officinarum* Poaceae) and tobacco (*Nicotiana tabacum* Solanaceae). Most cultivation involves slash-and-burn agriculture, known locally as tavy, in which farmers clear and burn native and secondary forests. Farmers plant various crops, mostly dry land rice and sugar cane, for *ca.* 3–5 yr and then abandon them for *ca.* 15 yr. Colonizing species, including woody plants such as *Harungana madagascariensis* (Clusiaceae), form a secondary thicket in abandoned cultivated areas. The tavy cycle is repeated until all vegetation is reduced to an impoverished secondary grassland. Forest habitats within the corridor are composed primarily of mid-altitude humid forests (Nicoll and Langrand, 1989), which tends to comprise endemic species of *Tambourissa* (Monimiaceae), *Ehippiandra* (Monimiaceae), *Ocotea* (Lauraceae), and *Breonia* (Rubiaceae). The shrub and herb layers include various species of Compositae, Rubiaceae, and Myrsinaceae. A high diversity of *Pandanus* sp. (Pandanaeae), bamboos (Poaceae), and epiphytic plants (Lowry *et al.*, 1997; Nicoll and Langrand, 1989) also exists. The canopy is continuous and low (*ca.* 12 m), and the tallest trees are 25 m.

We conducted surveys during 3 time periods at 7 sites: 1) October 25–November 3, 1999 at site 1, 2) February 15–April 2, 2000 at sites 2–6, and 3) June 1–October 29, 2003 and May 28–September 26, 2004 at site 7. We estimated anthropogenic disturbances—agriculture, selective logging, and hunting—at each site with data from direct observations, accounts of social scientists working in the survey areas (Lehman, 2000), and interviews with local people. We asked people ($N = 18$) to identify lemurs from illustrations in Mittermeier *et al.* (1994), including physical descriptions of each species,

and requested information on hunting techniques. Though it is ideal to measure the intensity of each response variable directly, many researchers use subjective measures or expert knowledge of anthropogenic disturbances in conservation biology (Bojorquez-Tapia *et al.*, 2003; Ricketts and Imhoff, 2003; Ricketts *et al.*, 1999) because of the difficulties in accurately measuring some variations, such as hunting pressures or a lack of time to conduct exhaustive scientific research or both (Davis *et al.*, 1990). For example, Peres and Dolman (2000) used subjective measures of primate hunting pressures over a 100-yr period for 56 sites in Brazilian Amazonia. To reduce inaccuracies inherent in the subjective measures (Bojorquez-Tapia *et al.*, 2003), only Lehman estimated intensities of anthropogenic disturbances. Following Peres and Dolman (2000), we used a 4-point intensity scale at each site:

1. None: Pristine sites with no current evidence of forest use—agriculture, deforestation, trails, cattle—or hunting activity
2. Light: Sites with low levels of forest use—limited agriculture, evidence for some selective tree extraction, i.e., stumps, small trails with complete canopy cover—no evidence of lemur traps but observations or reports of sporadic hunting by local people or both
3. Moderate: Sites with active logging, agriculture near edge habitats, and wide trails with some canopy openness, as well as reports or observations of consistent lemur hunting by local people, or both
4. Heavy: Sites subjected to continuous, persistent logging; intensive agriculture in all forest areas; active burning of forest habitats; broad trails with complete canopy openness; and direct evidence and reports of persistent and pervasive lemur hunting via traps, blow guns, and sling shots

We established 1–4 transects of varying length (300–2000 m) near each site (Table I). We did not standardize trail length because of the influence of deforestation, topography, limited time to cut new trails, and variations in altitude. We marked transects every 10 m with colored flagging tape. We used a Kestrel 4000 Weather Tracker (Nielsen-Kellerman, Nelson, PA) to collect data on altitude (m) every 100 m for each trail, and averaged the readings for each transect and then between each transect to provide a site-specific altitude value. We walked slowly (0.5–1.0 km/h) along each transect 2 times/d during times best suited for locating lemurs (0700–1100 h and 1400–1700 h). We conducted night surveys from 1900 to 2230 h. We collected data on date, time, transect number, participants, distance along trail, species/subspecies, group composition and size, sighting distance from trail at 90° height (m) of first individual, group spread (m), and method of detection—heard, saw, or smelled. Previous studies using similar methods revealed no sighting of new species after 5–15 h of diurnal surveys and 2–8 h of nocturnal surveys (Irwin *et al.*, 2005; Lehman, 2000; Schmid and

Table I. Survey effort, altitude, and evaluation of local habitats for 9 sites in SE Madagascar

Description	Bezavona	Garonina	Andrafasaka	Korikory	Ranomena	Mananjara	Vohibola	RNPb	Mantadia ^c
Site number	1	2	3	4	5	6	7	8	9
Altitude (m)	1223	1670	1685	1555	1345	1353	1311	1000	1075
No. transects	3	3	2	1	2	3	6	NA	NA
Transect length (km)	2.0	0.9	0.5, 1.0	1.3	1.2, 4.0	2.0	1.25	NA	NA
Survey distance (km)	32.0	10.0	10.5	23.9	17.2	33.9	518.7	NA	NA
Disturbance ^d									
Agriculture	Medium	High	High	Low	High	Medium	Low	Low	Low
Logging	High	High	Low	Low	High	High	Medium	Low	Low
Hunting	High	High	Low	Low	High	High	Medium	Low	Low

^aLow = insignificant impact/presence observed; medium = impact/presence observed; high = significant level of impact/presence observed.

^bData refer to main Talatekely camp for RNP (Wright, 1997).

^cData refer to research camp in northern section of Mantadia National Park (Powzyk, 1998; Powzyk and Mowry, 2003).

Rasoloarison, 2002; Sterling and McFadden, 2000; Sterling and Ramarason, 1996). Thus, the methods are applicable to determine specific richness but not specific density.

It is important to test and control for spatial autocorrelation when determining ecological correlates to biogeographic patterns (Fortin and Jacquez, 2000; Legendre and Fortin, 1989; Legendre *et al.*, 2002). Spatial autocorrelation is the pattern of relatedness of a set of spatially located data, the extent to which adjoining or neighboring spatial units are more likely to have similar magnitude than by chance alone (Fortin *et al.*, 2002). Spatial autocorrelation can inflate type I errors in statistical analyses and lead to false-positive results in correlations (Lennon, 2000). The spurious correlations can impact conservation efforts for endangered species (Diniz-Filho *et al.*, 2003). We conducted an *a priori* test for spatial autocorrelation via a Mantel test (Z), which is a linear estimate of the relationship between 2 square distance matrices of variables at the same sampling locations (Mantel, 1967). The first matrix was the Euclidean distance (km) between each site. The second contained the Sorenson's similarity index (SSI) for lemur species between each site, which we calculated as:

$$SSI = \frac{2C}{A + B}$$

where A is the total number of species at a site, B is the total number of species at another site, and C is the total number of species common to both sites. The index varies from 0 (sites contain no species in common) to 1 (sites contain same species). We then normalized the Mantel statistic (Z) into a correlation coefficient (r), which corresponds to the intensity of spatial autocorrelation for 2 variables (Fortin and Dale, 2005). We assessed statistical significance via a randomization technique with 1000 iterations (Legendre and Fortin, 1989). We conducted Mantel tests and associated significance values via Rndom Project (Jadwiszczack, 2002), and determined the correlation coefficient via the PopTools add-in for Excel (Hood, 2004). There is no evidence of spatial autocorrelation for our data on lemur diversity in SE Madagascar ($Z = 1867.8$, $r = 0.195$, $P = 0.38$), making controls for spatial autocorrelation unnecessary.

We used Spearman rank correlations (r_s) to determine if lemur diversity correlates with altitude or disturbance intensities—agriculture, selective logging, and hunting—or both for the 7 survey sites as well as lemurs at Ranomafana National Park (41,000 ha) and Mantadia National Park (15,500 ha). We chose the national parks because they are the closest protected areas to the corridor, have similar altitudinal levels and habitat types, contain all the taxa in the corridor, and maintain an intact lemur community that we assumed is free of lemur extirpations (Powzyk, 1998; White *et al.*, 1995; Wright, 1997). Thus, the null hypothesis to test is that there is

no difference in lemur community structure between sites in the corridor and those in nearby protected areas. We used 2-tailed statistical tests and an α level of 0.05.

RESULTS

We surveyed lemurs over 291.7 km at 7 sites in the corridor (Table II). We sighted 4 nocturnal taxa (*Avahi laniger*, *Cheirogaleus major*, *Lepilemur mustelinus*, and *Microcebus rufus*) and 6 diurnal taxa (*Eulemur rubriventer*, *E. fulvus rufus*, *E. f. fulvus*, *Propithecus diadema edwardsi*, *Hapalemur griseus griseus*, and *Varecia variegata variegata*). Lemur diversity ranged from a low of 2 taxa at Garonina to a high of 8 taxa at Vohibola (Table II). We sighted *Avahi laniger* at sites 4–8 ($N=90$ individuals), all of which are in the southern section of the corridor. We sighted *Cheirogaleus major* at 5 sites ($N=22$ individuals). Bite marks on tree branches and trunks indicated the possible presence of *Daubentonia madagascariensis* at 4 sites in the corridor (Bezavona, Garonina, Andrafisaka, and Korikory); however, we did not sight the species. We sighted *Eulemur fulvus fulvus* only at Bezavona ($N=4$ group sightings) and *E. f. rufus* only at Vohibola ($N=5$ group sightings). Average group size of *Eulemur fulvus fulvus* is $5.3 \pm .6$ individuals and for *E. f. rufus*, $3.2 \pm .8$. We sighted 104 *Eulemur rubriventer* at 5 sites (mean group size = $2.7 \pm .9$ individuals). *Hapalemur griseus griseus* was present at all sites except Bezavona and Garonina, and the average group size is 2.9 ± 1.6 individuals ($N=58$ group sightings). We observed *Lepilemur mustelinus* ($N=21$ individuals) at 3 sites (Garonina, Andrafisaka, and Vohibola). We surveyed *Microcebus rufus* ($N=139$ individuals) at all but 1 site (Korikory). We observed *Propithecus diadema edwardsi* only at the southern end of Vohibola ($N=17$ group sightings), and average group size is 3.29 ± 1.2 individuals. We surveyed 1 group of *Varecia variegata variegata* ($N=3$ individuals) at Mananjara.

We observed 2 groups of an apparently hybrid form of *Eulemur fulvus fulvus* and *E. f. rufus* at Bezavona. The body pelage of both the males and females was a light rufus color, easily distinguishable from the brown to the gray-brown color of *Eulemur fulvus fulvus*, but lighter than in *E. f. rufus* at Vohibola. The coat of most male *Eulemur fulvus fulvus* and *E. f. rufus* is brown to gray (Garbut, 1999; Mittermeier *et al.*, 1994; Tattersall, 1982). The black facial and head fur of the males was similar to that of *Eulemur fulvus fulvus*, but the collar, considerably fuller and whiter, resembled that of *E. f. rufus*. No individual had a red crown, as in *Eulemur fulvus rufus*. Males and females also had white eye patches similar to but slightly lighter than in *Eulemur fulvus fulvus*. No *Eulemur fulvus fulvus* in the area had discernible eye patches, as Mittermeier *et al.* (1994) suggested.

Table II. Lemur diversity for 9 sites in SE Madagascar

Lemur taxa	Site number ^d								
	1	2	3	4	5	6	7	8 ^b	9 ^c
<i>Avali laniger</i> (no. of ind.)	No	No	No	Yes (1)	Yes (1)	Yes (1)	Yes (3)	Yes (85)	Yes
<i>Cheirogaleus major</i> (no. of ind.)	Yes (4)	No	No	Yes (1)	Yes (1)	Yes (5)	Yes (6)	Yes (6)	Yes
<i>Daubentonia madagascariensis</i>	Yes (1)	Yes (1)	Yes (1)	Yes (1)	No	No	No	Yes	Yes
<i>Eulemur fulvus fulvus</i> (no. of groups)	Yes (4)	No	No	No	No	No	No	No	Yes
<i>E. f. rufus</i> (no. of groups)	No	No	No	No	No	No	Yes (5)	Yes	No
<i>E. f.?</i> (no. of groups)	Yes (2)	No	No	No	No	No	No	No	No
<i>E. rubriventer</i> (no. groups)	Yes (9)	No	Yes (1)	Yes (1)	Yes (1)	Yes (1)	Yes (1)	Yes (91)	Yes
<i>Haplemur aureus</i>	No	No	No	No	No	No	No	Yes	No
<i>H. griseus griseus</i> (no. of groups)	No	No	Yes (5)	Yes (2)	Yes (1)	Yes (2)	Yes (47)	Yes	Yes
<i>H. simus</i>	No	No	No	No	No	No	No	Yes	No
<i>Indri indri</i>	No	No	No	No	No	No	No	No	Yes
<i>Lepilemur microdon</i> (no. of ind.)	No	Yes (1)	Yes (1)	No	No	No	Yes (19)	Yes	Yes
<i>Microcebus rufus</i> (no. of ind.)	Yes (7)	Yes (3)	Yes (2)	No	Yes (7)	Yes (24)	Yes (96)	Yes	Yes
<i>Propithecus diadema diadema</i>	No	No	No	No	No	No	No	No	Yes
<i>P. d. edwardsi</i> (no. of groups)	No	No	No	No	No	No	Yes (17)	Yes	No
<i>Varecia variegata variegata</i> (no. of groups)	No	No	No	No	No	Yes (1)	No	No	No
Total no. of taxa	5(6)	3	5	5	5	6	8	11	10

^aNames for each site are located in Table I and (T) refers to trace evidence for this species.

^bData refer to main Talatekely camp for RNP (Wright, 1997).

^cData refer to research camp in northern section of Mantadia National Park (Powzyk, 1998; Powzyk and Mowry, 2003).

Table III. Spearman rank correlations between lemur diversity and anthropogenic disturbances in SE Madagascar

Variables	Agriculture	Logging	Hunting	Altitude
Lemur diversity	− 0.885 (0.002)	− 0.479 (0.192)	0.465 (0.207)	− 0.761 (0.017)
Agriculture	–	0.433 (0.244)	0.365 (0.335)	0.791 (0.011)
Logging		–	0.934 (0.001)	0.575 (0.136)
Hunting			–	0.044 (0.910)

Note. *P*-values are in parentheses. Statistically significant relationships are in bold.

Lemur diversity correlates negatively with agriculture intensity and altitude (Table III) for the 7 survey sites and 2 protected areas. For intersite comparisons of anthropogenic disturbances, hunting intensity covaries positively with logging intensity and agricultural intensity correlates positively with altitude.

DISCUSSION

Our first question involved determining the composition of the lemur community in the Fandriana-Marolambo forest corridor. It is broadly similar to that at other sites and protected areas in the region (Goodman and Shütz, 1999; Irwin *et al.*, 2005; Powzyk, 1998; Wright, 1997), with some notable exceptions. We sighted no *Hapalemur aureus* or *H. simus*. Moreover, no local person reported familiarity with the taxa, and the respondents were clear in their descriptions of *Hapalemur griseus griseus*. Other researchers did not find *Hapalemur aureus* or *H. simus* at sites 15–30 km south and north of the corridor (Goodman and Shütz, 1999; Irwin *et al.*, 2005; Lehman and Wright, 2000). We surveyed *Propithecus diadema edwardsi* only in the southernmost part of Vohibola, which is separated from the main corridor by large areas of grassland and cultivation. Other researchers observed *Propithecus diadema edwardsi* in the forest corridor 34 km south of Vohibola, which also contains Ranomafana National Park (Irwin *et al.*, 2005). The life-history characteristics of *Propithecus diadema edwardsi* make it particularly vulnerable to anthropogenic perturbation. *Propithecus diadema edwardsi* is the largest primate in SE Madagascar (5.0–6.0 kg) and is a favorite prey for local people (Lehman and Wright, 2000). It has a large home range (25–100 ha) and tends to live at low densities (8 individuals/km²) even in protected areas (Wright, 1995). *Propithecus diadema edwardsi* also has a low net reproductive growth rate owing to high infant and adult mortalities (Pochron *et al.*, 2004). Though we saw 1 group of *Varecia variegata variegata* at Mananjara, one should view the status of the group

as precarious given its proximity to a trail local people use. The raucous calls of the large (3.5–4.0 kg), conspicuous lemur make it easy for local people to hunt it throughout SE Madagascar (Ratsimbazafy, 2002). Other researchers did not observe *Varecia variegata variegata* at sites 22 km north of Bezavona (Goodman and Shütz, 1999; Rakotondraparany, 1997) and at 2 sites 34.7 kms south of Vohibola (Irwin *et al.*, 2005). Moreover, the large body size and distinctive vocalizations of *Propithecus diadema edwardsi* and *Varecia variegata variegata* make it unlikely that they were present but missed at our study sites (Lehman *et al.*, 2006-b). We did not sight *Indri indri* in the corridor. Previous studies in the region noted that the Mangoro River acts as a dispersal barrier to the taxon (Goodman and Ganzhorn, 2003). Conversely, our sighting of *Eulemur fulvus fulvus* at Bezavona further supports that the Onive River does not serve as a dispersal barrier for the taxon (Goodman and Ganzhorn, 2003). Though proving specific absence is an issue in studies that use survey methods (Buckland *et al.*, 1993), our lack of sightings and interview data support the restricted ranges of *Hapalemur aureus*, *H. simus*, *Propithecus diadema edwardsi*, *Varecia variegata variegata*, and *Indri indri* in SE Madagascar. Moreover, *Varecia variegata variegata* does not range into the Talatekely site in Ranomafana National Park or the research site in Mantadia National Park. Recent studies indicate that despite its absence in remote areas of Ranomafana, *Varecia variegata variegata* is sensitive to both natural, i.e., hurricane damage, and anthropogenic disturbances (Balko and Underwood, 2005; Ratsimbazafy, 2002).

Sightings of an apparently hybrid form of *Eulemur fulvus fulvus* and *E. f. rufus* may represent an important hybrid zone for lemurs. Johnson (2004), Sterling and Ramaroson (1996), and Wyner *et al.* (2002) have reported other *Eulemur fulvus* hybrid zones for white-collared brown lemurs (*E. f. albocollaris*) and collared brown lemurs (*E. f. collaris*) in SE Madagascar. Though Mittermeier *et al.* (1994) suggested that hybrid forms of *Eulemur fulvus fulvus* may exist in eastern Madagascar, researchers have thought the Onive River separates the taxa from conspecifics. Based on our surveys, the Onive River may not serve as an effective barrier to dispersal for *Eulemur fulvus fulvus*, and it may have hybridized with *E. f. rufus*. However, it is interesting that researchers surveyed no *Eulemur fulvus rufus* north of Vohibola, at the southernmost end of the corridor. Further surveys and genetic studies are needed to determine the extent of the hybrid zone and if the populations include hybrids.

Our second question related to determining correlates to lemur community structure. Altitude correlates with lemur diversity at the 9 sites in SE Madagascar. Six of the sites are below the maximum altitude (1600 m) for *Propithecus diadema edwardsi* (Goodman and Ganzhorn, 2003). Our sighting of *Varecia variegata variegata* at Mananjara (1353 m) marks the

maximum altitude for the species. Of the 8 sites we surveyed, 5 are ≤ 1353 m altitude. Maximum altitude limits for *Eulemur fulvus rufus* (1670 m) and *Avahi laniger* (1670 m) may explain their absence at Andrafisaka (1685 m). Thus, altitude and associated habitat affects may explain the absence of *Propithecus diadema edwardsi* at 2 sites (Garonina and Andrafisaka), *Varecia variegata variegata* at 3 sites (Garonina, Andrafisaka, and Korikory), and *Eulemur fulvus rufus* and *Avahi laniger* at 1 site (Andrafisaka) in the corridor.

Agricultural intensity covaries negatively with lemur diversity and positively with altitude for the 9 study sites. Despite a national moratorium on slash-and-burn agriculture, the practice occurs throughout the corridor. Slash-and-burn agriculture often occurs on steep slopes, many of which exceed 25° , which presumably leads to rapid soil loss during the annual rainy season. Local people reported that agricultural fields on such steep slopes can be used for only 1 or 2 growing seasons before they need to clear and burn new forest areas. Some people also use slash-and-burn agriculture to grow sugar cane for illegal production of rum, known as toaka gasy. Farmers have cleared numerous forest areas for sugar cane plantations near the southern end of the corridor, some of which are as large as 2.4 ha (Lehman, *unpubl. data*). Toaka gasy production leads to further forest destruction because people fell hard-wood trees for firewood and bark and also use leaves for flavoring during the fermentation process (Irwin and Ravelomanantsoa, 2004). They produce rum on site and then porters transport it in 25-liter containers for sale to individuals and markets. Interviews we conducted with local people at 2 villages (Ambohimotombo and Sahanato) near Vohibola indicated toaka gasy production and transportation are their primary source of hard currency. A market devoted exclusively to the sale of tokoa gasy is within walking distance of the corridor. Moreover, the tavy fields are being pushed progressively higher in altitude by local people throughout the corridor. Therefore, there is the very real possibility that primary forest may soon exist only in high-altitude areas but no lemurs may range into these habitats because they are at elevations above maximum species-specific limits in the corridor.

We also documented a strong positive correlation between intensities of selective logging and lemur hunting (Table III). Loggers typically hunt lemurs via blow guns, slingshots, and snare traps, as they do in many regions of Madagascar (Goodman and Raselimanana, 2003; Lehman and Wright, 2000; Müller *et al.*, 2000; Mutschler *et al.*, 2001). Although we did not document any correlation between lemur diversity and hunting pressures, it is important to note that correlations organize sampling entities along a gradient or continuum. However, some ecological variables, such as hunting, are neither linear or unidirectional (McGarigal *et al.*, 2000). Thus,

we made no statistical distinction between sites that may have high lemur densities that are not subject to hunting pressures and those with low lemur densities but high hunting pressures.

Though the Government of Madagascar is currently assessing the Fandriana-Marolambo forest corridor as a new national park, conservation plans for local lemurs are complicated by population isolation and determining the minimum size of the protected area. Isolation occurs because of the disjunct distribution of forest landscapes between the Fandriana-Marolambo forest corridor and the corridor that contains Ranomafana National Park (Fig. 1). Moreover, the Mangoro River is a major dispersal barrier to most lemurs at the northern end of the corridor (Goodman and Ganzhorn, 2003). Dispersal of lemurs from Ranomafana National Park into the corridor is unlikely because most species, including *Varecia variegata variegata*, seem unwilling or unable to traverse matrix habitats (Lehman *et al.*, 2006-a). Further, *Varecia variegata variegata* may no longer exist in the northern sections of Ranomafana (Irwin *et al.*, 2000), which further complicates natural dispersal. Though *Propithecus* sp. cross open areas ≤ 400 m between fragments (Lehman, *pers. obs.*), the question arises if individuals can successfully traverse the extensive open areas from sites south of the corridor. Ultimately, creation of a new protected area in all or part of the corridor requires conservation managers to determine how much habitat is enough to prevent lemur extirpations. For example, Gurd *et al.* (2001) compared mammal specific richness in eastern North American reserves to estimated species-area relationships before European settlement to determine if conservationists meet minimal area requirements for extant taxa. Of the 2355 reserves in the region, only 14 met or exceeded the minimum estimated required area to ensure no loss of mammal species. Their study accurately predicted the loss of mammal taxa in many protected areas in eastern North America. Researchers should conduct similar studies for lemurs and protected areas in SE Madagascar.

Presence-absence data are important for conservation biology (Brotons *et al.*, 2004; Gaston and Rodrigues, 2003; Rodrigues *et al.*, 2000), particularly when applied to studies of landscape processes, such as ours, and metapopulation dynamics (Cushman and McGarigal, 2004; Gilpin and Hanski, 1991; Hanski and Thomas, 1994). For example, Cushman and McGarigal (2004) found that presence-absence data effectively determined ecological correlates to bird community structure at the landscape level. However, presence-absence data are inherently limited in terms of determining clinal variations in response variables at the site level. For example, the 1 group of *Eulemur rubriventer* we sighted at Andrafsaka was equivalent to the 91 groups of conspecifics at Vohibola. Thus, it would be inappropriate to use our data to determine ecological correlates to

density variations for *Eulemur rubriventer* or any other lemurs in the corridor. Other researchers documented variations in primate densities at sites experiencing differing intensities of habitat disturbances (Chapman *et al.*, 2000; Lehman *et al.*, 2006-a; Paciulli, 2004). Moreover, each of these studies reported species-specific responses to habitat disturbances. For example, Lehman *et al.* (2006-a, 2006-b) found that *Avahi laniger* and *Microcebus rufus* existed at higher densities near forest edges whereas *Haplemur griseus griseus* tended to be omnipresent in Vohibola. Thus, a better understanding of lemur responses to altitude and anthropogenic factors will come from studies using both presence-absence data at the landscape level and density estimates at the site level.

There is a need for further surveys and increased site coverage to determine how species-specific lemur densities vary as a function of altitude and anthropogenic disturbances in the corridor. Quantification of anthropogenic response variables will enable researchers to determine causative rather than correlative relationships to lemur community structure. Finally, researchers need data on the minimum viable size of protected area to ensure that lemurs can survive in the Fandriana-Marolambo forest corridor.

ACKNOWLEDGMENTS

We thank the Association Nationale pour la Gestion des Aires Protégées, Ministère de L'Eau et de Forêt, L'Office National pour l'Environnement à Madagascar, and University of Antananarivo for permission to conduct research in Madagascar. We thank Patricia Wright and Benjamin Andriamahaja and the staff at MICET/ICTE for their support. We thank the people of Ambohimotombo, Fandriana, Andohariana, Ambinandrano, and Ankerana for their hospitality and support. We also acknowledge the bravery of the MICET RAP team members who weathered 2 hurricanes during research in the corridor. A previous version of the article benefited from the comments of 2 referees. The Madagascar National Office of the Environment, Saint Louis Zoological Park Field Research for Conservation Program, Primate Conservation Inc., Margot Marsh Biodiversity Foundation, Connaught Foundation, and a Discovery Grant from the Natural Sciences and Engineering Research Council of Canada supported the research.

REFERENCES

- ANGAP (2003). *Plan de Gestion du Réseau National des Aires Protégées de Madagascar*. Antananarivo, Madagascar: Association Nationale pour la Gestion des Aires Protégées, 113 pp.

- Balko, E. A., and Underwood, H. B. (2005). Effects of forest structure and composition on food availability for *Varecia variegata* at Ranomafana National Park, Madagascar. *Am. J. Primatol.* 66: 45–70.
- Bojorquez-Tapia, L. A., Brower, L. P., Castilleja, G., Sanchez-Colon, S., Hernandez, M., Calvert, W., Diaz, S., Gomez-Priego, P., Alcantar, G., Melgarejo, E. D., Solares, M. J., Gutierrez, L., and Del Lourdes Juarez, M. (2003). Mapping expert knowledge: Redesigning the monarch butterfly biosphere reserve. *Cons. Biol.* 17: 367–379.
- Brotos, L., Thuiller, W., Araujo, M. B., and Hirzel, A. H. (2004). Presence-absence versus presence-only modeling methods for predicting bird habitat suitability. *Ecography* 27: 437–448.
- Brummitt, N., and Lughadha, E. N. (2003). Biodiversity: Where's hot and where's not. *Cons. Biol.* 17: 1442–1448.
- Buckland, S. T., Burnham, K. P., Anderson, D. R., and Laake, J. L. (1993). *Density Estimation Using Distance Sampling*. London: Chapman & Hall.
- Chapman, C. A., Balcomb, S. R., Gillespie, T. R., Skorupa, J. P., and Struhsaker, T. T. (2000). Long-term effects of logging on African primate communities: A 28-year comparison from Kibale National Park, Uganda. *Cons. Biol.* 14: 207–217.
- Cushman, S. A., and McGarigal, K. (2004). Patterns in the species-environment relationship depend on both scale and choice of response variables. *Oikos* 105: 117–124.
- Davis, F. W., Stoms, D. M., Estes, J. E., Scepán, J., and Scott, J. M. (1990). An information systems approach to the preservation of biological diversity. *Int. J. Geogr. Inf. Syst.* 4: 55–78.
- Diniz-Filho, J. A. F., Bini, L. M., and Hawkins, B. A. (2003). Spatial autocorrelation and red herrings in geographical ecology. *Glob. Ecol. Biogeogr.* 12: 53–64.
- Du Puy, D., and Moat, J. (1996). *A refined classification of the primary vegetation of Madagascar based on the underlying geology: Using GIS to map its distribution and assess its conservation status*. In Proceedings of the International Symposium on Biogeography of Madagascar, pp. 205–218.
- Du Puy, D., and Moat, J. (1998). Vegetation mapping and classification in Madagascar (using GIS): Implications and recommendations for the conservation of biodiversity. In Huxley, C. R., Lock, J. M., and Cutler, D. F. (eds.), *Chorology, Taxonomy & Ecology of the Floras of Africa and Madagascar*. Royal Botanic Gardens, Kew, pp. 97–117.
- Fortin, M.-J., and Dale, M. R. T. (2005). *Spatial Analysis. A Guide for Ecologists*. Cambridge University Press, Cambridge, UK.
- Fortin, M.-J., Dale, M. R. T., and ver Hoef, J. (2002). Spatial analysis in ecology. In El-Shaarawi, A. H., and Piegorsch, W. W. (eds.), *Spatial Analysis in Ecology*. John Wiley & Sons, Chichester, pp. 2051–2058.
- Fortin, M.-J., and Jacquez, G. M. (2000). Randomization tests and spatially autocorrelated data. *Bull. ESA* 81: 201–206.
- G.E.F. (1996a). *Madagascar: Second Environment Program*. Global Environmental Facility (World Bank), Washington, DC, 166 pp.
- G.E.F. (1996b). *Third Environment Programme (EP III): United Nations Development Program and World Bank*, 164 pp.
- Ganzhorn, J. U., Langrand, O., Wright, P. C., O'Connor, S. O., Rakotosamimanana, B., Feistner, A. T. C., and Rumpfer, Y. (1996/1997). The state of lemur conservation in Madagascar. *Primate Cons.* 17: 70–86.
- Ganzhorn, J. U., Lowry, P. P., Schatz, G. E., and Sommer, S. (2001). The biodiversity of Madagascar: one of the world's hottest hotspots on its way out. *Oryx* 35: 346–348.
- Ganzhorn, J. U., Rakotosamimanana, B., Hannah, L., Hough, J., Iyer, L., Olivieri, S., Rajao-belina, S., Rodstrom, C., and Tilkin, G. (1997). Priorities for biodiversity conservation in Madagascar. *Primate Rep.* 48: 1–81.
- Ganzhorn, J. U., and Schmid, J. (1998). Different population dynamics of *Microcebus murinus* in primary and secondary deciduous dry forests of Madagascar. *Int. J. Primatol.* 19: 785–796.

- Garbut, N. (1999). *Mammals of Madagascar*. Pica Press, Sussex.
- Gaston, K. J., and Rodrigues, A. S. L. (2003). Reserve selection in regions with poor biological data. *Cons. Biol.* 17: 188–195.
- Gilpin, M., and Hanski, I. (1991). *Metapopulation Dynamics: Empirical and Theoretical Investigations*. Academic Press, London.
- Goodman, S., and Shütz, H. (1999). Observations of lemurs in the forest east of Tsinjoarivo, Ambatolampy. *Lemur News* 4: 14–16.
- Goodman, S. M., and Benstead, J. (2005). Updated estimates of biotic diversity and endemism for Madagascar. *Oryx* 39: 73–77.
- Goodman, S. M., and Ganzhorn, J. (2003). Biogeography of lemurs in the humid forests of Madagascar: The role of elevational distribution and rivers. *J. Biogeog.* 31: 47–56.
- Goodman, S. M., and Raselimanana, A. (2003). Hunting of wild animals by Sakalava of the Menabe region: A field report from Kirindy-Mite. *Lemur News* 8: 4–6.
- Green, G. M., and Sussman, R. W. (1990). Deforestation history of the eastern rain forests of Madagascar from satellite images. *Science* 248: 212–215.
- Gurd, D. B., Nudds, T. D., and Rivard, D. H. (2001). Conservation of mammals in eastern North American wildlife reserves: How small is too small? *Cons. Biol.* 15: 1355–1363.
- Hannah, L., Rakotosamimanana, B., Ganzhorn, J. U., Mittermeier, R. A., Olivieri, S., Iyer, L., Rajaobelina, S., Hough, J., Andriamialisoa, F., Bowles, I., and Tilkin, G. (1998). Participatory planning, scientific priorities, and landscape conservation in Madagascar. *Environ. Cons.* 25: 30–36.
- Hanski, I., and Thomas, C. D. (1994). Metapopulation dynamics and conservation: A spatially explicit model applied to butterflies. *Biol. Cons.* 68: 167–180.
- Harcourt, A. H., and Parks, S. A. (2003). Threatened primates experience high human densities: adding an index of threat to the IUCN Red List criteria. *Biol. Cons.* 109: 137–149.
- Hood, G. M. (2004). PopTools: 2.6.2. <http://www.cse.csiro.au/poptools>.
- Irwin, M. T., Johnson, S. E., and Wright, P. C. (2005). The state of lemur conservation in southeastern Madagascar: Population and habitat assessments for diurnal lemurs using surveys, satellite imagery and GIS. *Oryx* 39(2): 204–218.
- Irwin, M. T., and Ravelomanantsoa, H. V. (2004). Illegal rum production threatens health of lemur populations at Tsinjoarivo, eastern central Madagascar: Brief report and request for information. *Lemur News* 9: 16–18.
- Irwin, M. T., Smith, T. M., and Wright, P. C. (2000). Census of three eastern rainforest sites north of Ranomafana National Park: Preliminary results and implications for lemur conservation. *Lemur News* 5: 20–22.
- IUCN (2004). *IUCN Red List of Threatened Species*. IUCN Species Survival Commission, Gland, Switzerland.
- Jadwiszczack, P. (2002). Rndom projects: An application for randomization and bootstrap testing: 1.1. <http://pjadw.tripod.com/soft.htm>.
- Johnson, S. E. (2004). Ecology and speciation in brown lemurs: White-collared lemurs (*Eulemur albocollaris*) and hybrids (*Eulemur albocollaris* × *Eulemur fulvus rufus*) in southeastern Madagascar. Unpublished Ph.D. dissertation, University of Texas, Austin.
- Legendre, P., Dale, M. R. T., Fortin, M.-J., Gurevitch, J., Hohn, M., and Myers, D. (2002). The consequences of spatial structure for the design and analysis of ecological field surveys. *Ecography* 25: 601–616.
- Legendre, P., and Fortin, M.-J. (1989). Spatial pattern and ecological analysis. *Vegetatio* 80: 107–138.
- Lehman, S. M. (2000). *Final report on the rapid biological and socioeconomic assessments conducted in the Fandriana-Marolambo forest corridor in eastern Madagascar*. National Office of the Environment, Antananarivo, Madagascar, 156 p.
- Lehman, S. M. (2006). Conservation biology of Malagasy Strepsirhines: A phylogenetic approach. *Am. J. Phys. Anthropol* 130(2): 238–253.
- Lehman, S. M., Rajaonson, A., and Day, S. (2006-a). Edge effects and their influence on lemur density and distribution in southeast Madagascar. *Am. J. Phys. Anthropol* 129(2): 232–241.

- Lehman, S. M., Ratsimbazafy, J. H., Rajaonson, A., and Day, S. (2006-b). Decline of *Propithecus diadema edwardsi* and *Varecia variegata variegata* (Primates: Lemuridae) in south-east Madagascar. *Oryx* 40(1): 108–111.
- Lehman, S. M., and Wright, P. C. (2000). Preliminary description of the conservation status of lemur communities in the Betsakafandrika region of eastern Madagascar. *Lemur News* 5: 23–25.
- Lennon, J. J. (2000). Red-shifts and red herrings in geographical ecology. *Ecography* 23: 101–113.
- Lowry, P. P., Schatz, G. E., and Phillipson, P. B. (1997). The classification of natural and anthropogenic vegetation in Madagascar. In Goodman, S. M., and Patterson, B. D. (eds.), *Natural Change and Human Impact in Madagascar*. Smithsonian Institution Press, Washington, DC, pp. 93–123.
- Mantel, N. (1967). The detection of disease clustering and a generalized regression approach. *Cancer Res.* 27: 209–220.
- McGarigal, K., Cushman, S., and Stafford, S. (2000). *Multivariate Statistics for Wildlife and Ecology Research*. Springer, New York.
- Mittermeier, R. A., Konstant, W. R., Nicoll, M. E., and Langrand, O. (1992) *Lemurs of Madagascar: An Action Plan for Their Conservation 1993–1999*. IUCN, Gland, Switzerland.
- Mittermeier, R. A., Tattersall, I., Konstant, W. R., Meyers, D. M., and Mast, R. B. (1994). *Lemurs of Madagascar*. Conservation International, Washington, DC.
- Müller, P., Velo, A., Raheliarisoa, E.-O., Zaramody, A., and Curtis, D. (2000). Surveys of sympatric lemurs at Anjamena, north-west Madagascar. *Afr. J. Ecol.* 38: 248–257.
- Mutschler, T., Randrianarisoa, A. J., and Feistner, A. T. C. (2001). Population status of the Alaotran gentle lemur *Haplemur griseus alaotrensis*. *Oryx* 35: 152–157.
- Nicoll, M. E., and Langrand, O. (1989). *Madagascar: Revue de la Conseration et des Aires Protégées*. WWF, Gland, Switzerland.
- Paciulli, L. M. (2004). The effects of logging, hunting, and vegetation on the densities of the Pagai, Mentawai Island primates (Indonesia). Unpublished Ph.D. dissertation, SUNY—Stony Brook, Stony Brook.
- Peres, C. A., and Dolman, P. M. (2000). Density compensation in neotropical primate communities: Evidence from 56 hunted and nonhunted Amazonian forests of varying productivity. *Oecologia* 122: 175–189.
- Pochron, S. T., Tucker, W. T., and Wright, P. C. (2004). Demography, life history, and social structure in *Propithecus diadema edwardsi* from 1986–2000 in Ranomafana National Park, Madagascar. *Am. J. Phys. Anthropol.* 125: 61–72.
- Powzyk, J. A. (1998). The socio-ecology of two sympatric indrids, *Propithecus diadema diadema* and *Indri indri*: A comparison of feeding strategies and their possible repercussions on species-specific behaviors. Unpublished Ph.D. dissertation, Duke University, Durham.
- Powzyk, J. A., and Mowry, C. B. (2003). Dietary and feeding differences between sympatric *Propithecus diadema diadema* and *Indri indri*. *Int. J. Primatol.* 24: 1143–1162.
- Rakotondraparany, F. (1997). *Inventaire faunistique de la Forêt Naturelle de Tsinjoarivo-Ambatolampy*. Antananarivo: Projet de Développement Forestier Intégré dans la région du Vakinankaratra, GTZ.
- Ratsimbazafy, J. (2002). On the brink of extinction and the process of recovery: Responses of black-and-white ruffed lemurs (*Varecia variegata variegata*) to disturbance in Manombo Forest, Madagascar. Unpublished Ph.D. dissertation, Stony Brook University, Stony Brook, NY.
- Ricketts, T., and Imhoff, M. (2003). Biodiversity, urban areas, and agriculture: Locating priority ecoregions for conservation. *Cons. Ecol.* 8: 1–15.
- Ricketts, T. H., Dinerstein, E., Olson, D. M., Loucks, C., Eichbaum, W., Kavanagh, K., Hedao, P., Hurley, P., Carney, K. M., Abel, R., and Walters, S. (1999). *Terrestrial Ecoregions of North America: A Conservation Assessment*. Island Press, Washington, DC.
- Rodrigues, A. S., Gaston, K. J., and Gregory, R. D. (2000). Using presence-absence data to establish reserve selection procedures that are robust to temporal species turnover. *Proc. Roy. Soc. Lond. B Biol. Sci.* 267: 897–902.

- Rowe, N. (1996). *The Pictorial Guide to the Living Primates*. Pogonias Press, East Hampton.
- Schmid, J., and Rasoloarison, R. M. (2002). Lemurs of the Réserve Naturelle Intégrale d'Ankarafantsika, Madagascar. In Alonso, L. E., Schulenberg, T. S., Radilofe, S., and Missa, O. (eds.), *A Biological Assessment of the Réserve Naturelle Intégrale d'Ankarafantsika, Madagascar*. Conservation International, Washington, DC, pp. 73–82.
- Sechrest, S., Brooks, T. M., da Fonseca, G. A. B., Konstant, W. R., Mittermeier, R. A., Purvis, A., Rylands, A. B., and Gittleman, J. L. (2002). Hotspots and the conservation of evolutionary history. *Proc. Natl. Acad. Sci. USA* 99: 2067–2071.
- Sterling, E., and McFadden, K. (2000). Rapid census of lemur populations in the Parc National de Marojejy, Madagascar. *Fieldiana Zool.* 97: 265–274.
- Sterling, E. J., and Ramarason, M. G. (1996). Rapid assessment of the primate fauna of the eastern slopes of the Réserve Naturelle Intégrale d'Andringitra, Madagascar. *Fieldiana Zool.* 85: 293–305.
- Tattersall, I. (1982). *The Primates of Madagascar*. Columbia University Press, New York.
- Vallan, D. (2002). Effects of anthropogenic environmental changes on amphibian diversity in the rain forests of eastern Madagascar. *J. Trop. Ecol.* 18: 725–742.
- White, F. J., Overdorff, D. J., Balko, E. A., and Wright, P. C. (1995). Distribution of ruffed lemurs (*Varecia variegata*) in Ranomafana National Park, Madagascar. *Fol. Primatol.* 64: 124–131.
- Wolfheim, J. C. (1983). *Primates of the World: Distribution, Abundance, and Conservation*. University of Washington Press, Seattle.
- Wright, P. C. (1995). Demography and life history of free-ranging *Propithecus diadema edwardsi* in Ranomafana National Park, Madagascar. *Int. J. Primatol.* 16: 835–854.
- Wright, P. C. (1997). The future of biodiversity in Madagascar: A view from Ranomafana National Park. In Goodman, S. M., and Patterson, B. D. (eds.), *Natural Change and Human Impact in Madagascar*. Smithsonian Institution Press, Washington, DC, pp. 381–405.
- Wyner, Y. M., Johnson, S. E., Stumpf, R. M., and Desalle, R. (2002). Genetic assessment of a white-collared × red-fronted lemur hybrid zone at Andringitra, Madagascar. *Am. J. Phys. Anthropol.* 57: 51–66.