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Source: Primate Conservation, 22(1) : 71-77

Published By: Conservation International

URL: <https://doi.org/10.1896/052.022.0105>

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The Status of Lemur Species at Antserananomby: An Update

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Abstract: Antserananomby Forest was once a refuge of the rare deciduous flora of western Madagascar. Through primate studies that were conducted in the late 1960s and early 1970s, it was discovered that the primate density and diversity in this forest was greater than any other known in western Madagascar. Although research at Antserananomby ceased in the 1980s, satellite images from 2000 indicated that the forests were still intact. In August 2004, we returned to Antserananomby to determine whether this site could feasibly become a location for long-term primate research and to assess whether efforts should be initiated to establish Antserananomby Forest as a national reserve. In addition to general assessments, we conducted diurnal primate surveys using the line transect sampling method. We found that the 8.6 ha of Antserananomby Forest have since been cleared. Due to recent demographic and attitudinal changes in the local human population, the surrounding forests are regularly burned, and at least some of the lemur species are hunted with lemur traps, dogs, and sling shots. In addition, the population densities of especially *Eulemur fulvus rufus* and *Lemur catta*, but also of *Propithecus verreauxi verreauxi*, *Phaner furcifer*, and *Lepilemur ruficaudatus*, have declined appreciably. We conclude that although all of the primate fauna appear to be present, the current rate of deforestation at Antserananomby is unsustainable. If no action is taken to conserve what is left and restore what has been lost, then the forests in this region and their inhabitants are likely to soon disappear.

Key Words: Madagascar; deforestation; sacred forests; critically endangered ecoregion

Introduction

The region of Antserananomby is 12 km north of the Mangoky River, 21.7°S, 44.1°E, in the Toliara province of Madagascar (Fig. 1). In the 1970s, one of the forests, Antserananomby, was the site of a comparative primate ecology study and several primate surveys (Petter *et al.* 1971; Sussman 1972; Richard 1978). Antserananomby was an alluvial forest of dense, mainly deciduous vegetation with trees reaching a height of 25 to 30 m. The dominant tree was *Tamarindus indica*, but species such as *Acacia royumae*, *Ficus soroceoides*, *Terminalia mantaly*, *Quivisia the papinae*, and *Vitex beraviensis* were also relatively common (Sussman 1972).

Within the last thirty years, there has been very little contact between the villagers of Antserananomby and researchers. In addition to Sussman, the villagers remember Otto Appert, a Swiss missionary and naturalist who lived close to the area for many years. Appert produced multiple publications on bird species in the region (for example, Appert 1968, 1970a, 1970b, 1980), and one broad diurnal primate survey (Appert

1966). One of the main reasons so few other researchers have conducted studies in this area is that the entire region north of the Mangoky River becomes an island throughout the austral summer, when the Mangoky and Morondava rivers swell from the rains. In addition, the ability to reach Antserananomby has become increasingly problematic with the region's continuous decline in infrastructure (Sussman *et al.* 2003).

Despite its inaccessibility, Antserananomby has long been perceived as a site of great ecological importance. Specific to the primate fauna, Antserananomby has been the only forest found to contain all of the lemur species known to exist in this region of western Madagascar [Sussman, unpubl. data]. Moreover, the densities of these populations have been reported as exceptionally high. When A. Schilling and Sussman conducted surveys on *Lepilemur ruficaudatus* (red-tailed sportive lemurs) and *Phaner furcifer* (western fork-marked lemur) in the late 1960s, they found densities of 260 individuals/km² and at least 550 individuals/km² respectively (Petter *et al.* 1971). Similarly, Sussman (1972, 1974) observed that *Lemur catta* lived in densities of 214 individuals/km² and that *Eulemur*

fulvus rufus lived in densities of 1,120 individuals/km². Both densities are the highest ever recorded for any unprovisioned *L. catta* and *E. f. rufus* populations (Sussman 1972; Gerson 1999; Overdorff *et al.* 1999; Sussman *et al.* 2006). Last, in 1974, A. Richard accompanied Sussman to Antserananomby Forest and identified 86 *Propithecus verreauxi verreauxi* in mean group sizes of 7.8 (Richard 1978), with a conservative density estimate of 860 individuals/km². These numbers are the highest mean group size and density numbers recorded for these taxa (Table 1).

At the time of these studies, it was not only the researchers who recognized the value of Antserananomby Forest. The people of this region were also aware of Antserananomby Forest's richness and would mention this forest whenever they were asked about local plants or animals. Hunting was forbidden



Figure 1. Location of Antserananomby.

within its boundaries by the inhabitants of the neighboring village (Antserananomby) because it was perceived as a sacred site (Sussman 1972).

In an effort to conserve the area's unique flora and fauna, Sussman and colleagues Ian Tattersall and Joelisoa Ratsirason recently planned to begin the process to establish Antserananomby Forest and the surrounding forests as a national reserve. These plans were encouraged by satellite images from 2000, which indicated that the forests of Antserananomby, including Antserananomby Forest, were still intact (Sussman *et al.* 2003). In 2001 and 2004, surveys were conducted to ground truth the information conveyed by the satellite images. During our surveys, however, we found that conditions in the region had changed radically since the 1970s–1980s. A number of major socio-economic changes had transformed the region, including the immigration of people who did not respect the taboos (*fadys*) of the previous local inhabitants and the introduction of new crops. In this paper, we present a vivid example of how drastic changes can occur within a very short period of time, forever eliminating unique ecological communities and habitats. Many of the extremely rich but small, mainly undisturbed, natural habitats are not perpetuated as recognized protected reserves but, instead, by the beliefs and practices of the local people (Smith 1997; Clark *et al.* 1998; Golding and Folke 2000; Harpet *et al.* 2000; Casse *et al.* 2004; Bodin *et al.* 2006; Green *et al.* unpubl. ms.). A greater attempt must be made to protect these areas. As stated by Smith (1997: pp.438 & 440) “It is evident that in Madagascar, as in many countries, reserves have been primarily located in areas unsuitable—or least suitable—for alternative use and development. This strategy is likely to have caused the extinction of many species and the loss of some of the best examples of Western dry forest.”

Methods

Earlier censuses were conducted at Antserananomby by Sussman and colleagues in 1970 and 1974. In 1970, all groups of *L. catta* and *E. f. rufus* living within the 9–10 ha gallery forest at Antserananomby were censused weekly or bi-weekly between July and September. There were 12 groups of red-fronted lemur with a total of approximately 112 animals, and 1 group of ringtailed lemurs containing 19 individuals (Sussman 1972). In 1974, all groups of *P. v. verreauxi* inhabiting the same forest were identified and then censused repeatedly by A. Richard and R. W. Sussman during the month

Table 1. Density estimates of *Propithecus v. verreauxi* and *Eulemur fulvus rufus* in the surrounding forests of the former site of Antserananomby.

	No. of inds. observed	No. of inds. analyzed	Transect width m	Mean group size	95% CI of mean group size range	Mean ind. per km ²	95% CI of inds. per km ²	Pop. densities from previous studies in SW Madagascar ¹
<i>P. v. verreauxi</i>	134	89	59	3.6	3.2–4.1	49.0	36.0–66.7	80–550 ²
<i>E. f. rufus</i>	58	47	25	2.7	2.2–3.4	24.0	15.4–37.0	90–1120 ³

¹Previous estimates of ringtailed lemur density in undisturbed forest are 75–300 individuals per km² (Sussman *et al.* 2006).

²Richard (1978), Jolly *et al.* (1982), Richard *et al.* (1997).

³Smith (1991), Sussman (2003).

of July. There were 10 groups with a total of 58 individuals (Richard 1978). The forest was in a circumscribed area with a relatively low continuous canopy with exceptional visibility, and groups were easily observed and censused.

In August 2004, Kelley and Muldoon revisited Antserananomby to 1) determine whether this site could feasibly become a location for long-term ecological research and to 2) assess whether efforts to establish Antserananomby Forest as a national reserve should continue. In addition, we conducted a diurnal primate survey using Buckland *et al.*'s (2001) line-transect sampling method (see also Burnham and Anderson 1976; Burnham *et al.* 1980). This method was chosen over other methods, such as point transects, because line transect surveys are ideal for animals such as primates that 1) typically occur in low densities, 2) have large home ranges, and 3) are difficult to detect unless disturbed (Whitesides *et al.* 1988; Buckland *et al.* 2001; Ross and Reeve 2003). Since the gallery forest at Antserananomby no longer existed, the methods used in earlier years were no longer feasible. Permission to conduct this study was granted through the University of Antananarivo. The data collection methods are in compliance with the legal requirements for ecological research in Madagascar. Here we report on the census data collected on the diurnal lemur species in 2004.

Data collection

Data collection for the line-transect surveys took place from 8 August 2004 to 27 August 2004. A total of 122 hours were spent collecting line transect data within a total area of 5.9 km². The hours of data collection coincided with the diurnal/cathemeral lemurs' peak activity (Sussman 1972; Ganzhorn 1995; Müller *et al.* 2000). Morning data were collected from 06:30 to 12:30. At 1500, we would survey a different forest fragment because it minimized the risk that the same group would be counted twice in the same day (Ross and Reeve 2003). We collected afternoon data until approximately 18:00 hr. For each lemur sighting, we collected the following data: a) the time of sighting, b) Geographic Positioning System (GPS) readings (latitude, longitude, elevation, accuracy), c) the distance between us and the individual or central member in the group of lemurs, d) the number of observed adults and sub-adults, e) the initial canopy height of the lemurs, f) the compass direction the team was traveling when the lemur(s) were spotted, g) the compass direction of the lemur(s) in relation to the field team, and h) the compass direction the lemur(s) were traveling if they were moving when seen. Notes on general behavior were also recorded *ad libitum*. Only actual sightings were counted (Ganzhorn 1995; Müller *et al.* 2000). If we suspected that a group or individual had already been counted, we did not record that sighting.

Data analysis

GPS data on lemur sightings were plotted on a LANDSAT 7 ETM + image to indicate where these groups were found relative to: 1) the Ianandranto River, the only water source, 2) villages, and 3) other landmarks. Measurement errors were

corrected by referring to notes on landscape features that fell within the accuracy ranges measured by the GPS.

Density estimates for *P. v. verreauxi* and *E. f. rufus* were analyzed using Distance 5.0 Beta 5 (Thomas *et al.* 2005). The sample size of *L. catta* was too low for this analysis (Buckland *et al.* 2001). Prior to density analyses, sightings distance data were visualized in box plots and histograms using SPSS 11.5. Based on these results, the observation width for *P. v. verreauxi* was truncated to 59 m, and the observation width for *E. f. rufus* was truncated to 25 m. Density estimates were obtained using the uniform + cosine (Fourier series) estimator (Crain *et al.* 1979; Burnham *et al.* 1980; Buckland *et al.* 2001). Group size and density estimates were the same regardless of whether group size estimates were obtained using mean cluster size or the size-regression method.

Results

Upon arrival at Antserananomby, it immediately became apparent that a great deal of change had occurred in the region since the 1970s (Fig. 2). First, the site of the old Antserananomby village is now barren savanna. Second, Antserananomby Forest is gone. Third, lemur traps, of which we observed four, were found within the remaining fragmented forests.

Seven of the eight lemur species that were known to inhabit Antserananomby Forest were observed during the survey, however: *E. f. rufus*, *L. catta*, *L. r. ruficaudatus*, *Microcebus murinus*, *Mirza coquereli*, *P. fuscifer*, and *P. v. verreauxi*. The only species that was not sighted, *Cheirogaleus medius*, hibernates during the austral winter (Sussman 1972; Hladik *et al.*, 1980).

Since surveys were conducted only during the day, density estimates were not obtained for the nocturnal species. Among the three diurnal/cathemeral species, *P. v. verreauxi* was the most frequently sighted and widely dispersed. Over half of the 202 group sightings (which sometimes consisted of a single individual) were of Verreaux's sifaka ($n = 134$), and four sifaka females were observed with infants. While the mean observed group size for this species was 3.6 (Table 1), one group contained 12 individuals. This species could be observed as far as 250 m away in the hillier areas of the region. In addition, *P. v. verreauxi* was the only species to be observed in groups of three or more within 500 m of Antserananomby village. As of 2004, we estimate the population density of Verreaux's sifaka at Antserananomby to be 49 individuals/km². The second most frequently sighted of the three species was *E. f. rufus* ($n = 58$). These sightings often consisted of a lone individual or a pair, although the average group size was slightly higher (Table 1). The population density of this species was estimated to be 23.9 individuals/km². *Lemur catta* was only observed 10 times. With the exception of a troop that we sighted almost 125 m away, the species reacted to our presence every time. Consequently, half of the *L. catta* sightings were of a single individual ($n = 5$).

Most notable during the surveys were the observations of two mixed species groups. In this context, we have defined



Figure 2. Comparison of the general Antserananomby area. Figure 2a was taken on the dried Beangily river bed and is an image of Antserananomby Forest in 1970. Figure 2b is a view of the same general area in 2004 as it looked from the bank of the Beangily River. Notice the fire smoldering across the remaining forest fragments in the 2004 photograph.

mixed-species groups as groups with individuals of two species that travel, feed, and/or rest together as would one with individuals of a single species. Both groups that met this definition were seen together more than once over a 24-hour time period. The first group, of five Verreaux's sifakas and three red-fronted lemurs, was observed in a continuous canopy forest fragment just five minutes from camp. This forest fragment was near a burning forest patch, and parts of the forest near the camp were also smoldering. One of the two *E. f. rufus* infants that were sighted during the survey was observed in this group. The second mixed group was of seven red-fronted lemurs and eight ringtailed lemurs. It was seen traveling and feeding near the Ianadranto River, the only running water in the region during the austral winter. This mixed-species group had the largest number of *E. f. rufus* found near this river, and the only young ringtailed lemur seen throughout the study. Last, it is of interest to note that the second time the second group was observed, it was seen traveling through the exact same location with the same number of individuals, but with a single Verreaux's sifaka tailing the group.

Discussion

Primate survey

Based on six years of observations, Appert (1966) wrote that the most widespread and frequently sighted of the diurnal primate species in the Mangoky/Antserananomby region was Verreaux's sifaka, and the least frequently sighted was the red-fronted lemur. Although it does not appear that Appert surveyed our area, our results are relatively consistent. Since in western Madagascar red-fronted lemurs are restricted largely to the dense middle canopies of deciduous and gallery forests (Sussman 2003; Müller *et al.* 2000), habitat type may be an important reason why the red-fronted lemur had a high local density at Antserananomby Forest but not elsewhere.

However, the results of our survey clearly indicated that the overall densities of red-fronted lemurs and ringtailed

lemurs have declined appreciably within the last few decades. Even Verreaux's sifaka, which appeared to be faring somewhat better relative to the other two species in this region, was found at a much lower density than is typical for this species (49 individuals/km² compared with 80–550 individuals/km², Table 1), when approximately 30 years earlier it had the highest recorded density for sifakas (Sussman 2003). Similarly, although we did not systematically conduct nocturnal surveys, due to the complete loss of rich gallery forest habitat where the high density of these species was observed in earlier surveys, there is no doubt that the *L. ruficaudatus* and *P. furcifer* populations have also declined markedly. These two species are largely restricted to undisturbed primary canopy forests in this region (Smith *et al.* 1997, Sussman pers. obs.).

Last, we believe that the mixed species groups are the residual results of crowding (Hagan *et al.* 1996). In the example of the sifaka and red-fronted lemur group, fires were burning in the surrounding forest fragments. It is likely that what was observed was a demographic "concussion" in which individuals from both species were forced to reside within the same fragmented forest patch (Hagan *et al.* 1996). This is the only group of red-fronted lemurs that was found near camp. Similarly, since running drinking water is very important for red-fronted lemurs (Scholz and Kappeler 2004); it is of note that the mixed species group that inhabited the fragment by the river had the largest number of *E. f. rufus*. It is possible that cohabitation with *L. catta* was the best opportunity these red-fronted lemurs had for gaining access to the water.

Causes of the recent changes at Antserananomby

Appert (1966) noted unsustainable rates of deforestation within the Mangoky/Antserananomby region as early as the 1960s. Antserananomby Forest was always an exception, however, because it was protected by the local villagers (Sussman, 1972). There is evidence that the causes for the forest's recent demise are human migration and the introduction of maize.

In the late 1970s, many of the original inhabitants of Antserananomby Village died from an epidemic disease, and the village was abandoned (Sussman unpubl. data), and the town of Vondrove, which used to be the closest center of economic activity to Antserananomby, also started to decline (Sussman *et al.* 2003). Today, all that remains of Vondrove is a small village. The Antserananomby area, which has been sparsely inhabited for many years, has recently been resettled by immigrants who lack the restrictions on clearing the forest and hunting the lemurs that were maintained by earlier inhabitants (R. W. and L. K. Sussman, unpubl. data). Given this, it is interesting to note that Verreaux's sifaka, the largest and most visible species at this site, is also the only species that could readily be found resting there, and at ease in close proximity to the village.

In addition, maize is a new crop to Antserananomby that was not present during the 1970s research (R. W. and L. K. Sussman, unpubl. data). Unlike crops such as cassava and sweet potatoes, maize requires *hatsaka* (Horning 2000; Horning 2003; Sussman *et al.* 2003). *Hatsaka* is a type of slash-and-burn agriculture in which forests are cut in one to six ha patches and burned (Ferguson 2002; Sussman *et al.* 2003; Casse *et al.* 2004). As this agricultural practice is technically illegal in Madagascar, *hatsaka* is more commonly practiced in isolated areas (Jarosz 1993; Casse *et al.* 2004). Economists who have studied the effects of maize cropping south of the Antserananomby region have found that *hatsaka* is the primary reason for forest clearance [Casse *et al.* 2004]. During our 2004 survey, *hatsaka* was the major crop in the area surrounding Antserananomby. Although maize was not yet being grown on the plot that was once the Antserananomby gallery forest, future maize cropping is undoubtedly the reason for its recent clearance (Bernard Tsiefatao pers. comm.).

Conclusions

In the volume accompanying the vegetation map published in 1965, Humbert and Cours Darne described the type of forest represented by Antserananomby Forest as almost totally destroyed with only rare vestiges still remaining (Humbert, 1965, p.70). Moreover, deciduous dry forests in Madagascar have declined from 12.5% of the original cover in 1950 to only 2.8% in 1990 (Smith, 1997, p.426). Since Antserananomby Forest and some of the remaining forests were likely included in the 1990 percentage, its recent disappearance suggests that current estimates of remaining dry forests in Madagascar are even smaller.

Since forest regeneration in southwest Madagascar is slow to non-existent once large portions of a forest have been cleared (Sussman *et al.* 2003; Casse *et al.* 2004), future conservation efforts at Antserananomby could serve as a case study for whether an environment that has rapidly degenerated in recent years can be repaired. In the best case scenario, future research with applied conservation efforts at Antserananomby could result in environmentally sustainable sustenance alternatives for the local human population, the protection

of lemur species, and the initiation of collaborative interests among the local community, the Malagasy government, and the scientific community. Yet achieving these aims will be a major challenge. Logistically, this area is often inaccessible for nine months of the year and a follow-up attempt to visit this site in 2005 failed, partly because of its remoteness. In addition, it is possible that the densities of some of the primate species, most notably red-fronted lemurs and ringtailed lemurs are already too low for successful recovery. Yet if the remaining forests in the region of Antserananomby disappear, then the region's villagers will likely have to move to forested areas with fertile land, if any still exist, where the destructive processes that are occurring at Antserananomby will be perpetuated. Conserving what is left of the region's biodiversity will not only benefit the immediate area, it will also benefit three of the world's most unique and critically endangered ecosystems—the spiny and succulent xerophytic forests of southern Madagascar, the rapidly disappearing deciduous forests of the northwest, and especially the extremely rare, lush forests of the small transition area that contains the unique flora and fauna between the two.

The loss of the gallery forest of Antserananomby offers another example of the importance of local beliefs and practices, and of “sacred forest” in the preservation of small but extremely rich and unique ecological communities and habitats throughout Madagascar and elsewhere. In the region between the Morondava and Mongoky rivers, we are observing a rich and unique habitat disappear before our eyes. The question is whether anything can, or will, be done to prevent this irreversible tragedy.

Acknowledgments

Transportation, letter of intent, and permission to conduct this research was provided by the University of Antananarivo's School of Agronomy, notably by Prof. Joelisoa Ratsirason. We warmly thank him for his support and assistance. Ony Andrianasolondraibe played an integral role at the field site as translator, and her assistance in collecting the data is greatly appreciated. We also thank Brad Kelley and two anonymous reviewers who gave us very useful suggestions. This project was supported in part by the Washington University Anthropology Summer Travel Grant [EAK]. We wish to thank Washington University's Graduate School of Arts and Sciences for providing this funding. This project adhered to the research protocols of Madagascar.

Literature Cited

- Appert, O. 1966. La distribution géographique des lemuriens diurnes de la région du Mangoky au sud-ouest de Madagascar. *Bull. l'Académie Malgache* 44: 43–45.
- Appert, O. 1968. Neues zur lebensweise und verbreitung des kurols, *Leptosomus discolor* (Hermann). *J. Ornithologie* 109: 116–126.

- Appert, O. 1970a. Zur biologie der Vangawürger (Vangidae) südwest-Madagaskars. *Der Ornithologische Beobachter* 67: 101–133.
- Appert, O. 1970b. Zur biologie einiger kua-arten Madagaskars. *Zoologische Jahrbücher. Abteilung für System* 97: 424–453.
- Appert, O. 1980. Erste farbaufnahmen der rachenzeichnung junger kuas von Madagaskar (Cuculi, Couinae). *Der Ornithologische Beobachter* 77: 85–101.
- Bodin, Ö, M. Tengö, A. Norman, J. Lundberg and T. Elmqvist. 2006. The value of small size: Loss of forest patches and ecological thresholds in southern Madagascar. *Ecol. Applications* 16: 440–451.
- Buckland, S. T., D. R. Anderson, K. P. Burnham, J. L. Laake, D. L. Borchers and L. Thomas. 2001. *Introduction to Distance Sampling*. Oxford University Press, Oxford.
- Burnham, K. P. and D. R. Anderson. 1976. Mathematical models for nonparametric inferences from line transect data. *Biometrics* 32: 325–336.
- Burnham, K. P., D. R. Anderson and J. L. Laake. 1980. Estimation of density from line transect sampling of biological population. *Wildl. Monog.* 72: 1–202.
- Casse, T., A. Milhøj, S. Ranaivoson and J. R. Randriamanarivo. 2004. Causes of deforestation in southwestern Madagascar: What do we know? *For. Policy. Econ.* 6: 33–48.
- Clark, C. D., S. M. Garrod and M. Parker Pearson. 1998. Landscape archaeology and remote sensing in southern Madagascar. *Int. J. Remote Sensing* 19: 1461–1477.
- Crain, B. R., K. P. Burnham, D. R. Anderson and J. L. Laake. 1979. Nonparametric estimation of population density for line transect sampling using Fourier series. *Biom. J.* 21: 731–748.
- Ferguson, B. 2002. *Opportunities for Community Based Conservation in the Androy Region of Madagascar's Southern Spiny Forest*. The Tandroy Conservation Trust, Ifotaka, Androy, Madagascar. 25pp.
- Ganzhorn, J. U. 1995. Low-level forest disturbance effects on primary production, leaf chemistry, and lemur populations. *Ecology* 76: 2084–2096.
- Gerson, J. S. 1999. Social relationships in wild red-fronted lemurs (*Eulemur fulvus rufus*). Doctoral dissertation, Duke University, Durham, NC.
- Golding, J. and C. Folke. 2000. The taboo system: lessons about informal institutions for nature management. *The Georgetown International Law Review* 12: 413–445.
- Green, G. M., R. W. Sussman and S. P. Sweeney. Undated. Stability in a convolving mosaic of land-cover change episodes: conservation by sacred forests in southwestern and southern Madagascar. Unpublished manuscript.
- Hagan, J. M., W. M. V. Haegen and P. S. McKinley. 1996. The early development of forest fragmentation effects on birds. *Conserv. Biol.* 10: 188–202.
- Harpert, C., J. Vololoniaina and C. M. Hladik. 2000. Sacred lemur sites in the Sakalava region of north-west Madagascar; updated data and implications for sustained development and conservation. *Rev. d'Ecol., La Terre et la Vie* 55: 291–295.
- Hladik, C. M., P. Charles-Dominique and J. J. Petter. 1980. Feeding strategies of five nocturnal prosimians in the dry forest of the west coast of Madagascar. In: *Nocturnal Malagasy Primates: Ecology, Physiology, and Behavior*, P. Charles-Dominique, H. M. Cooper, A. Hladik, C. M. Hladik, E. Pages, G. F. Pariente, A. Petter-Rousseaux, J. J. Petter (eds.), pp.41–73. Academic Press, New York.
- Horning, N. R. 2000. Explaining compliance with rules governing common-pool forest resource use and conservation: dynamics in Bara country, southwestern Madagascar. *Meetings paper for the International Association for the Study of Common Property*, Bloomington, Indiana 31 May – 4 June 2000. 29pp. Available at: <<http://dlc.dlib.indiana.edu/archive/00000569/00/horningn052300.pdf>>. Accessed 26 January 2007.
- Horning, N. R. 2003. How rules affect conservation outcomes. In: *The Natural History of Madagascar*, S. M. Goodman and J. P. Benstead (eds.), pp.146–153. The University of Chicago Press, Chicago, IL.
- Humbert, H. 1965. Description des types de végétation. In: *Notice de la Carte Madagascar*, H. Humbert and G. Cours Darne (eds.), pp.46–78. L'Institut Francais de Pondichery, Pondichery.
- Jarosz, L. 1993. Defining and explaining tropical deforestation: shifting cultivation and population growth in colonial Madagascar (1896–1940). *Econ. Geogr.* 69: 366–379.
- Jolly, A., H. Gustafson, W. L. R. Oliver and S. M. O'Connor. 1982. *Propithecus verreauxi* population and ranging at Berenty, Madagascar. 1975 and 1980. *Folia Primatol.* 39: 124–144.
- Müller, P, A. Velo, E. O. Raheliarisoa, A. Zaramody and D. J. Curtis. 2000. Surveys of sympatric lemurs at Anjamena, north-west Madagascar. *Afr. J. Ecol.* 38: 248–257.
- Overdorff, D. J., P. T. Merenlender, A. Telo and Z. A. Forward. 1999. Life history of *Eulemur fulvus rufus* from 1988–1998 in southeastern Madagascar. *Am. J. Phys. Anthropol.* 108: 295–310.
- Petter, J. J., A. Schilling and G. Pariente. 1971. Observations eco-ethologiques sur deux lemuriens Malgaches nocturnes: *Phaner furcifer* et *Microcebus coquereli*. *Extrait de la Terre et la Vie* 3: 287–327.
- Richard, A. F. 1978. *Behavioral Variation: Case Study of a Malagasy Lemur*. Associated University Presses, Inc., Cranbury, NJ.
- Richard, A. F., P. Rakotomanga and M. Schwartz. 1993. Dispersal by *Propithecus verreauxi* at Beza Mahafaly, Madagascar. *Am. J. Primatol.* 30: 1–20.
- Ross, C. and N. Reeve. 2003. Survey and census methods. In: *Field and Laboratory Methods in Primatology*, J. M. Setchell and D. J. Curtis (eds.), pp.90–109. Cambridge University Press, Cambridge, UK.
- Scholz, F. and P. M. Kappeler. 2004. Effects of seasonal water scarcity on the ranging behavior of *Eulemur fulvus rufus*. *Int. J. Primatol.* 25: 599–613.

- Smith, A. P. 1997. Deforestation, fragmentation, and reserve design in western Madagascar. In: *Tropical Forest Remnants: Ecology, Management, and Conservation of Fragmented Communities*, W. F. Lawrence and R. O. Bierregaard Jr. (eds.), pp.415–441. The University of Chicago Press, Chicago, IL.
- Smith, A. P., N. Horning and Moore, D. 1997. Regional biodiversity planning and lemur conservation with GIS in western Madagascar. *Conserv. Biol.* 11: 498–512.
- Sussman, R. W. 1972. An ecological study of two Madagascan primates: *Lemur fulvus rufus* (Audebert) and *Lemur catta* (Linnaeus). Doctoral dissertation, Duke University Durham, NC.
- Sussman, R. W. 1974. Ecological distinctions in sympatric species of *Lemur*. In: *Prosimian Biology*, R. D. Martin, G. A. Doyle, A. C. Walker (eds.), pp.75–108. Duckworth, London.
- Sussman, R. W. 2003. *Primate Ecology and Social Structure*, Vol. 1. Pearson Custom Publishing, Needham Heights, MA.
- Sussman, R. W., G. M. Green, I. Porton, O. L. Andrianasolondraibe and J. Ratsirarson. 2003. A survey of the habitat of *Lemur catta* in southwestern and southern Madagascar. *Primate Conserv.* (19): 32–57.
- Sussman, R. W., S. Sweeney S, G. M. Green, I. Porton, O. L. Andrianasolondraibe and J. Ratsirarson. 2006. A preliminary estimate of *Lemur catta* population density using satellite imagery. In: *Ring-tailed Lemur Biology*, A. Jolly, R. W. Sussman, N. Koyama, and H. R. Rasamimanana (eds.), pp.16–31. Springer, New York.
- Thomas, L., J. L. Laake, S. Strindberg, F. F. C. Marques, S. T. Buckland, D. L. Borchers, D. R. Anderson, K. P. Burnham, S. L. Hedley, J. H. Pollard, J. R. B. Bishop and T. A. Marques. 2005. Distance 5.0. Release Beta 5. Research Unit for Wildlife Population Assessment, University of St. Andrews, St. Andrews, UK: Available at: <<http://www.ruwpa.st-and.ac.uk/distance/>>. Accessed 14 February 2007.
- Whitesides, G. H., J. F. Oates, S. M. Green and R. P. Kluber-danz. 1988. Estimating primate densities from transects in a West African rain forest: A comparison of techniques. *J. Anim. Ecol.* 57: 345–367.

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Received for publication: 12 March 2007

Revised: 29 June 2007

