

# Global population size of a critically endangered lemur, Perrier's sifaka

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## Keywords

*Propithecus perrieri*; survey; population density; geographic distribution; conservation status.

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## Abstract

The Perrier's sifaka *Propithecus perrieri*, considered critically endangered by the IUCN (World Conservation Union; 2004), is one of the least studied and most endangered primates in the world, yet baseline information on its distribution and population levels has not been updated for over 10 years. Density estimates from former studies suggest that only between 100 and 2000 individuals remain in the wild. In 2003–2004, using the line-transect method, information on the distribution and population levels of this and sympatric primate species were obtained. Multi-spectral, Landsat 7 satellite images of areas comprising the known Perrier's sifaka distribution, acquired in 1994 and 2002, were compared using spatial analysis techniques to quantify regional patterns of deforestation. Results from this study indicate that the global population of the Perrier's sifaka consists of about 915 individuals and the effective population size is unlikely to exceed 230 individuals. Furthermore, an annual deforestation rate of 1.2% was detected in the only protected area where this species occurs. Deforestation, the decline of taboos against hunting and human immigration patterns influence primate population status in northern Madagascar and threaten to drive the Perrier's sifaka to extinction in the near future.

## Introduction

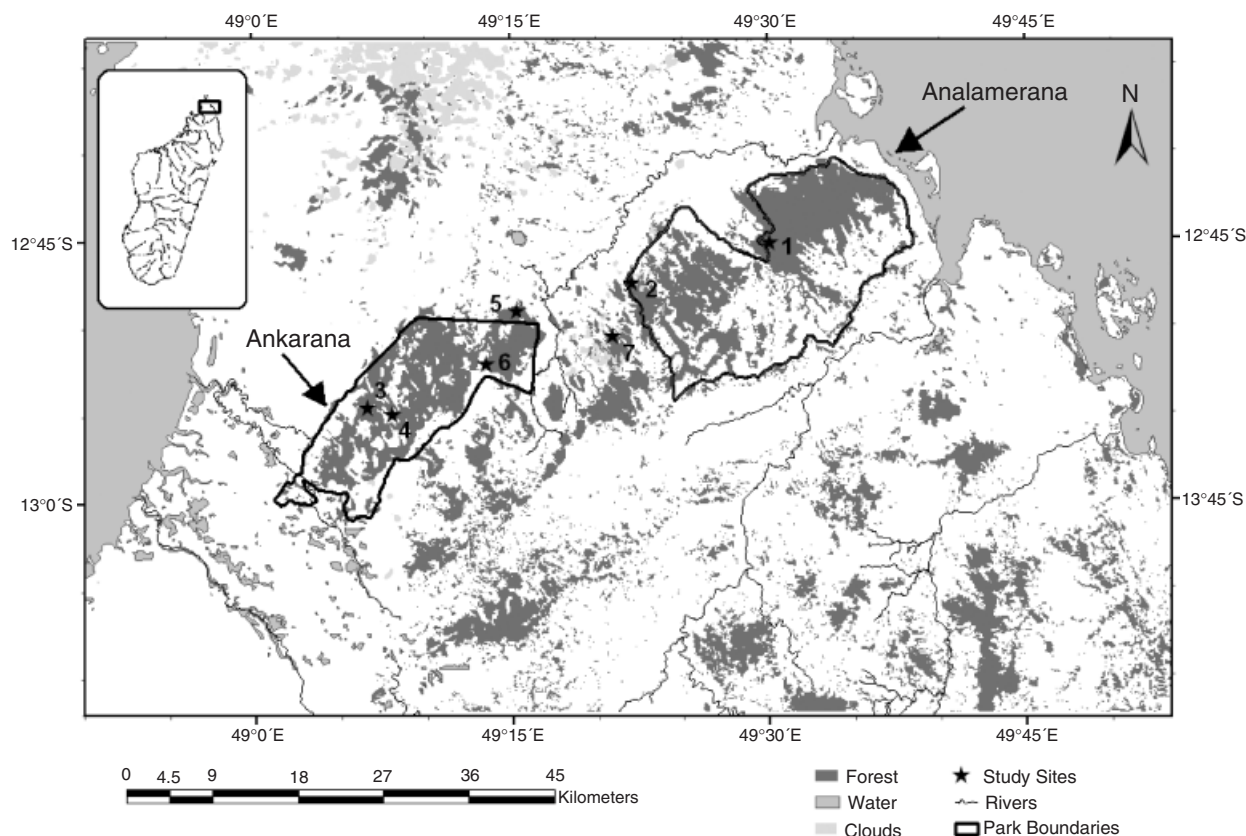
Madagascar is one of the world's top conservation priorities (Myers *et al.*, 2000; Mittermeier, Konstant & Rylands, 2003). The decline of the country's entirely endemic primate fauna has closely tracked the tremendous rates of forest removal that have fragmented a once largely forested landscape (Green & Sussman, 1990; Nelson & Horning, 1993; Dufils, 2003). A number of authors have acknowledged that many of the island's diverse lemur species are at considerable risk of extinction (Jernvall & Wright, 1998; Ganzhorn *et al.*, 2001; Mittermeier *et al.*, 2006a). Efforts to fill gaps in our knowledge of lemur population status and ecology have been propelled to the forefront of national conservation management strategies (Wright & Jernvall, 1999; Ganzhorn *et al.*, 2001; Mittermeier *et al.*, 2003).

Perrier's sifaka *Propithecus perrieri*, a strepsirrhine primate, is classified as critically endangered by the IUCN (Baillie, Hilton-Taylor & Stuart, 2004; Mittermeier *et al.*, 2006b). Weighing between 3.7 and 5.0 kg (Lehman, Mayor & Wright, 2005), this deciduous dry forest sifaka is primarily folivorous (Lehman & Mayor, 2004) and exhibits a vertical clinging and leaping form of locomotion. Even the earliest published studies of behaviour and ecology have acknowledged the species' rarity and that its small range makes it susceptible to habitat modification and destruction (Petter,

Albignac & Rumpler, 1977; Le Normand, 1988). Perrier's sifakas are threatened by swidden agriculture, wildfires, sapphire and hardwood extraction as well as hunting throughout their range (Meyers & Ratsirarson, 1989; Mayor & Lehman, 1999). A recent analysis examining the phylogenetic relationships among known *Propithecus* spp. that drew from morphological and genetic evidence supported the elevation of *Propithecus diadema perrieri* to specific status, as *P. perrieri* (Mayor *et al.*, 2004).

Historically, the geographic range for *P. perrieri* includes only the very restricted area of dry forests that occurs within the Analamerana Special Reserve (hereafter Analamerana) and possibly sections of the neighbouring Ankarana Special Reserve (hereafter Ankarana; see Fig. 1; Hawkins *et al.*, 1990). Recently it has been suggested that *P. perrieri* may be found in only one protected area, Analamerana (Mittermeier *et al.*, 2003), although newer reports document the presence of Perrier's sifakas in some of the unprotected forests lying between these two protected areas (Mittermeier *et al.*, 2006b).

Previous efforts to estimate the population size of *P. perrieri* indicate that the total remaining number of individuals is small, at levels from anywhere between 100 and 2000 individuals (Petter *et al.*, 1977; Meyers & Ratsirarson, 1989; Mayor & Lehman, 1999). In 1977, Petter and colleagues suggested that at densities of only 3–4 individuals km<sup>-2</sup>, the total population of Perrier's sifakas was



**Figure 1** Location of primate survey sites in northern Madagascar. Site names: 1, Analabe; 2, Ankavana; 3, Anilotra; 4, Deuxieme Rivière; 5, Mahory/Nosibe; 6, Sentier Botanique; 7, Ambery.

then unlikely to exceed 1000 individuals. More recent survey results provided density estimates of 20 individuals  $\text{km}^{-2}$  (Meyers & Ratsirarson, 1989). Coupled with presence-absence data in areas within and bordering the 34 700 ha Analamerana, these authors concluded that about 2000 individuals may have then remained in the wild. Since then, *P. perrieri* has also been seen during surveys conducted in 1987 (Hawkins *et al.*, 1990) within the boundaries of Ankarana, although too few sightings of *P. perrieri* at Ankarana were recorded to derive density estimates and it is unclear whether these encounters were with vagrant animals.

Three diurnal primate species are sympatric with Perrier's sifakas: crowned lemurs *Eulemur coronatus*, Sanford's brown lemurs *Eulemur sanfordi* and western bamboo lemurs *Hapalemur occidentalis*. The latest IUCN Red List assessments classify both *E. coronatus* and *H. occidentalis* as vulnerable and *E. sanfordi* as endangered (Baillie *et al.*, 2004). Both the high conservation value of these taxa and earlier suggestions that sympatric primates may compete with Perrier's sifakas (Meyers & Ratsirarson, 1989) warrant their inclusion in systematic surveys aimed at clarifying Perrier's sifaka population levels.

In this study we first attempted to survey the existing *P. perrieri* and sympatric primate populations in Analamerana, Ankarana and bordering areas to estimate population densities and distribution. We then compared our current

estimates of population size for the *P. perrieri* population with that of previous survey efforts. Additionally we have assessed patterns of forest loss from 1988 to 2003 using satellite images. Finally, by placing these findings within the broader context of the current conservation status of and existing threats to Perrier's sifaka's, we provide updated recommendations for the long-term management of this species.

## Materials and methods

### Study sites

Surveys of diurnal lemurs, with special emphasis on *P. perrieri*, were conducted by M. A. B., E. R. E. and A from 10 June to 30 August 2003 and from 26 September and 11 November 2004. Surveys were conducted at seven different sites in northern Madagascar: two in Analamerana, four in Ankarana and one in an unprotected forest neighbouring these reserves. At the two Analamerana sites, 'intensive surveys' (sites 1 and 2) were conducted over periods of 25 days or more using line transects to obtain estimates of population density (individuals  $\text{km}^{-2}$ ), while at the remaining five sites matching techniques were implemented over shorter periods (5–6 days) to determine encounter rates (groups  $\text{km}^{-1}$ ).

In June and July 2003, our first intensive survey site, Analabe (Fig. 1, site 1), was visited. This site is located in the easternmost forest block of the reserve at 12°45S 49°30E. Forests rise along sheer, rocky escarpments of eroded limestone and persist along the banks of the Bobokindro River, a waterway that dissects this forest block along its western edge from north-west to south-east. Riparian forests situated directly alongside the Bobokindro were cleared during the middle of the 20th century to install a telephone line from the city of Antsiranana in the extreme north to Voehemar on the north-east coast of the island. Clearings that remain are frequently travelled by transient immigrants, miners and other foot travellers. The density of human population is low here, but regenerating forests found along the western banks of the Bobokindro are a reminder of persistent hardwood extraction and remnant plots from swidden agriculture.

We visited the forests of Ankavana (Fig. 1, site 2; 12°48S 49°22E) along the Ankavana River, in the reserve's second largest forest block, during August 2003. Elaborate canals have been established here by diverting the tributaries toward lowland areas used in paddy rice production. Villagers regularly visit the forests to maintain the integrity of canals, and individuals encountered claimed to hold a local taboo or *fady* against hunting lemurs. Nevertheless, it is clear that the ethnic make-up of these communities is changing, and while traditionally observed by members of the local Antakarana tribe, this *fady* is not practised by members of other ethnic groups immigrating to this part of Madagascar. Forest edges were noticeably influenced by fire here and in some cases evidence of recent burning encroached several hundred metres within the forest interior.

Five additional sites located both within and bordering Ankarana were visited between September and November 2004 to conduct rapid primate surveys (Fig. 1, sites 3–7). The first of these sites that was visited, Anilotra (12°54S 049°06E; site 3), is situated in the interior of Ankarana and supports dry deciduous forest. A large road passes through Anilotra and tourists and park officials are a conspicuous presence here. Large (~1–2 m in diameter and depth) man-made holes were discovered along major routes, most likely for the purpose of harvesting tenrecs (Tenrecidae), but no other evidence of illegal activity was recorded here.

A second site within Ankarana's interior was also visited, located at 12°54S 049°08E, and known in published accounts as Deuxieme Riviere (site 4). Xerophytic and deciduous forests are found here (Hawkins *et al.*, 1990). Former trails used to access this site were overgrown and appeared not to have been used in several years. Only much older signs of human disturbance were recorded here, including felled trees and overgrown routes likely used for selective logging.

Two sites located in the north-eastern section of Ankarana were visited. These sites support semi-evergreen forests. The site of Mahory/Nosibe (12°48S 049°15E; site 5) comprises part of the same forest block as site 6, the Sentier Botanique, yet is situated further north. Large clearings interrupt degraded semi-evergreen forest here. Direct evi-

**Table 1** Summary table of census effort at intensive (sites 1–2) and rapid survey sites (sites 3–7)

Site name (number)	Transect name	Transect length (km)	Repetitions (#)	Survey effort (km)
Analabe (1)	Analabe West I	3.6	9	32.4
Analabe (1)	Analabe West II	4.5	13	58.5
Analabe (1)	Analabe East I	3	13	42
Analabe (1)	Analabe East II	4.5	9	40.5
Ankavana (2)	Ankavana I	3.9	25	96.9
Ankavana (2)	Ankavana II	4.2	20	83.5
Anilotra (3)	Anilotra I	2.8	6	16.7
Deuxieme	Deuxieme	2.7	6	15.9
Riviere (4)	Riviere I			
Mahory/Nosibe (5)	Mahory I	3.6	4	14.4
Sentier	Sentier	3.6	6	21.3
Botanique (6)	Botanique I			
Ambery (7)	Ambery I	2.4	6	14.1
Ambery (7)	Ambery II	0.5	4	2.0

dence of hardwood extraction was recorded and some tree holes had also been excavated to capture torpid animals for food. The northernmost 3.1 km<sup>2</sup> of this site is not part of the reserve. The Sentier Botanique (12°52S 049°13E; site 6) is found within a few kilometres of Ambondromifehy, a town that received a large influx of illegal sapphire miners during the mid-1990s (Cardiff & Befourouack, 2003). Levels of human disturbance were high here and indirect signs of hunting tree-hole dwelling primates were evident. Illegal squatters harvesting hardwoods were also encountered during surveys.

The last site visited for rapid primate surveys is situated between Ankarana and Analamerana at 12°50S 049°20E and is known as the Ambery forest (site 7). This site receives no official protection, but village leaders have begun discussing management possibilities with regional park officials. Active *tavys* or plots used in swidden agriculture, evidence of recent fire as well as the large struts used to extract hardwoods were found here.

## Abundance estimates

At all sites visited, transects were established along existing trails and frequently covered both sides of major waterways. Primate populations were surveyed using the line-transect method and our methodology followed that of previous researchers (NRC, 1981; Whitesides *et al.*, 1988; Johnson & Overdorff, 1999). Transects varied in length (3.0–4.5 km) and were walked during the morning (06:00–11:00 h) and afternoon (13:30–17:35 h). At the five rapid primate survey sites (sites 3–7) the encounter rates (i.e. groups km<sup>-1</sup>) are reported. Survey effort for all study sites is summarized in Table 1. During the intensive surveys, information on activity, height, age class, sex, group composition, slope of the terrain and level of forest degradation as described by Ganzhorn *et al.* (1997) were recorded during sighting events.

Tests of inter-observer reliability were conducted on a monthly basis (Martin & Bateson, 1993).

The distance from the observer of an encountered primate was estimated either by sight or (for distances greater than 15 m) with an optical rangefinder. Perpendicular animal-path distances were calculated for the first animal seen using the following equation:  $p = d \sin \alpha$ , where  $d$  = distance from observer and  $\alpha$  = detection angle (Borries *et al.*, 2002). Following Whitesides *et al.* (1988), these distances were subsequently transformed into estimates of the perpendicular distance to the centre of each group encountered.

Transect width was calculated for each species encountered using the histogram inspection technique and a 50% criterion for falloff distance (Whitesides *et al.*, 1988; Fashing & Cords 2000; Irwin, Johnson & Wright, 2005). Survey area was derived by multiplying survey width by total transect length. Species densities were then calculated using the following equation:

$$\text{Density} = I/2EL_t$$

where  $I$  is the number of individuals observed,  $E$  is the effective distance (km) and  $L_t$  is the total transect length (i.e. transect length number of repetitions) (Whitesides *et al.*, 1988; Johnson & Overdorff, 1999; Irwin *et al.*, 2005). We chose not to use distance sampling techniques for our analysis because the number of sightings for each species did not approach the recommended sample sizes (Buckland *et al.*, 1993). At each site, average density estimates (means) were tabulated across each individual transect or path surveyed. The density estimates reported here were then determined by calculating mean population densities from these mean site densities. We estimated the total population size for the Perrier's sifaka by multiplying the mean density across sites by the area of total habitat available (described below). In addition, we used the rule of thumb suggested by Cowlshaw & Dunbar (2000) to estimate the effective population size as one quarter of the survey population.

To establish the validity of pooling data from repeat walks of the same transects at our intensive study sites (sites 1–2), we investigated whether the time of day the transect was walked, or the direction it was walked, had any influence on the frequency of primate sightings. We found no effect of either time (morning/afternoon) or direction (eastwards/westwards) on sighting frequency (Wilcoxon matched-pair tests:  $n = 5-18$ ,  $P > 0.15$  in all cases). Because our transects were of variable length, we also assessed whether the density estimates from different transect segments showed any difference. No differences were found ( $\chi^2$  tests: Analabe  $\chi^2 = 0.480$ ,  $P = 0.997$ ; Ankavana  $\chi^2 = 0.592$ ,  $P = 0.991$ ). As a result, all the transect data were pooled (see Whitesides *et al.*, 1988).

### Spatial analysis

Landsat 7 satellite images comprising seven spectral layers were obtained from the global land cover facility, maintained by the University of Maryland. Images were selected to include the entire area of distribution reported for the

Perrier's sifaka in surveys conducted by Meyers & Ratsirarson (1989) in the late 1980s. These authors conducted a very comprehensive survey of forests in northern Madagascar by exploring northern and southern limits to this species' range and by considering geographic barriers in their assessments. Although this study is now over 10 years old, these data offer a useful baseline for subsequent updates. A time series for habitats within this area was also established by choosing multiple images, separated by a minimum of eight years. We selected images for this analysis that possessed minimal cloud cover to better facilitate our interpretation of landscape features. To minimize differences arising from seasonal changes in leaf cover, all the images used in this analysis were acquired during the pronounced 8-month dry season that extends from April to November in this part of Madagascar.

We used Erdas Imagine 8.6© to derive a supervised classification from the spectral signature of each Landsat 7 image that distinguished forest from non-forest (Irwin *et al.*, 2005). 'Ground truthing' exercises were conducted using a hand-held Global Positioning System (GPS) unit during visits to various habitat types within the region. In addition, strong visible differences between forest and non-forest areas as represented in raw images suggest that we were able to reliably distinguish between these habitat types (see Irwin *et al.*, 2005). Subsets of the original images were prepared in order to isolate the area comprising the known distribution for Perrier's sifaka. We converted these images to polygon coverages using ArcGIS 9© software and generated unique layers for such landscape features as rivers, coastlines, park boundaries and roads.

In order to provide area estimates for habitats considered important and available to Perrier's sifakas given their current geographic range, coverages were 'clipped' to include such habitats as they occur both within and outside park boundaries. We also calculated the proportion of these habitats that are represented by fragments of 1 km<sup>2</sup> or less using the patch analysis extension of ArcView/ArcGIS 9 ©. Based on both previous surveys and biodiversity monitoring exercises initiated by Association Nationale pour la Gestion des Aires Protégées (ANGAP) since 1997, Perrier's sifakas have been found using riparian and dry deciduous forests (Lehman & Mayor, 2004). Perrier's sifakas have been seen crossing open areas to reach neighbouring forest fragments (Mayor & Lehman, 1999), and the greatest distances covered fall within the range of 600 m. As such, only riparian and dry deciduous forests located within 600 m of known source populations were included in our area calculations.

To track patterns of forest loss since 1989, the period of the last *P. perrieri* surveys (Meyers & Ratsirarson, 1989), we compared forest cover estimates between Landsat 7 images acquired in 1994 and 2002. Patterns were less clear in Ankarana, presumably the result of reflectance from the more exposed escarpments of limestone karst here and our inability to obtain satellite images for this reserve that were consistently acquired during the dry season. Therefore, we decided to exclude images depicting Ankarana in our analysis.

**Table 2** Summary table of studies on *Propithecus perrieri* population levels

Study	Locality	Sites	Survey methods	Individuals km <sup>-2</sup>	Survey effort (km)	Group size	Estimated population size
Petter <i>et al.</i> (1977)	Analamera	NA	NA	3–4	NA	3–4 adults	< 1000
Meyers & Ratsirarson (1989)	Analamera	Analabe (1), Ankavana (2) and Anjakely	IS and RS	20	56	3–6 adults	2000
Mayor & Lehman (1999)	Analamera	Antobiratsy	B	NA	NA	3–4 adults	NA
Current study	Analamera	Analabe (1) and Ankavana (2)	IS	3.11 (SE = 0.9)	359.68	2–5 adults	915

Where sites are shared between past censuses and the current study, site numbers are provided in parentheses.

IS, intensive survey/census methods; RS, rapid survey/census methods; B, behavioral studies.; NA, information not available.

## Results

### Transect results

#### Population densities at Analamerana

Estimated population densities varied across species at both the sites visited. At both sites, observations of *P. perrieri*, *E. coronatus* and *E. sanfordi* were recorded. Densities for *P. perrieri* were low at these sites (Analabe:  $2.2 \pm 0.7$  individuals km<sup>-2</sup>; Ankavana:  $5.2 \pm 1.1$  individuals km<sup>-2</sup>) and differ from past survey efforts (Table 2). When data from surveys at both sites are pooled for *P. perrieri*, we arrive at an estimate of  $3.1 \pm 0.9$  individuals km<sup>-2</sup>. Pooled densities for Sanford's brown lemur *E. sanfordi* were also very low at both the Analabe ( $5.5 \pm 1.8$  individuals km<sup>-2</sup>) and Ankavana forests ( $3.5 \pm 1.7$  individuals km<sup>-2</sup>). Only the crowned lemur *E. coronatus* reached higher population levels at both sites where primates were intensively surveyed (Analabe:  $25.2 \pm 4.6$  individuals km<sup>-2</sup>; Ankavana:  $21.2 \pm 4.0$  individuals km<sup>-2</sup>).

At both sites, flight was frequently recorded during encounters with Perrier's sifakas as a response to observers (number of encounters: *P. perrieri*: 29 of 35). Groups of *P. perrieri* typically moved well beyond both the visual and auditory range of observers on contact, but occasionally other reactions to observers were recorded. This included the concerted retreat of the group to areas outside the visual detection of observers but to areas where animals could still be heard alarm calling. In other but less frequent instances ( $n = 4$ ), the adult males of sifaka groups remained within close proximity of observers (i.e. 10 m or less) and even approached with heads raised and shaking from side to side in an agitated fashion. In other encounters ( $N = 2$ ), sifaka groups appeared indifferent to the presence of observers. This response occurred only when considerable distances (i.e. > 20 m) separated the sifakas from observers and during the early mornings, when temperatures were lowest. Crowned lemurs and Sanford's brown lemurs also responded by fleeing from observers during encounters (number of encounters: *E. coronatus*: 18 of 80; *E. sanfordi*: four of 20). Additionally, groups of these species ceased moving in response to observers in a smaller number of encounters (i.e. *E. coronatus*: five of 80 encounters; *E. sanfordi*: two of 20

encounters). In 60 of 135 encounters with all primates, the habitat was considered disturbed, with evidence of selective logging or other human activities.

#### Rapid primate surveys: encounter rates

All rapid primate survey sites (sites 3–7), with the exception of Ambery (site 7) and northern sections of the Mahory/Nosibe (site 6) locality, are part of the Ankarana Special Reserve. There were significant differences in the rate of encounters for primate species across these 5 sites (Kruskal–Wallis;  $H = 15.014$ ,  $P < 0.01$ ).

No group of *P. perrieri* was sighted within the boundaries of the Ankarana Special Reserve (Table 3). Perrier's sifaka was encountered during our transect walks on one occasion (yielding an encounter rate of 0.06 groups km<sup>-1</sup>) at Ambery, an isolated series of forest fragments located between Ankarana and Analamerana. The species was also seen three more times at this site, outside of systematic transect walks. Animals fled on all these occasions.

A single group of *H. occidentalis* was observed during our visit to Ambery, a secondary forest site supporting patches of giant bamboo (*Valiha* sp.). During our sole encounter with this species, the sighted group dispersed widely and high into the canopy while alarm calling and waving their tails from side to side in an agitated manner.

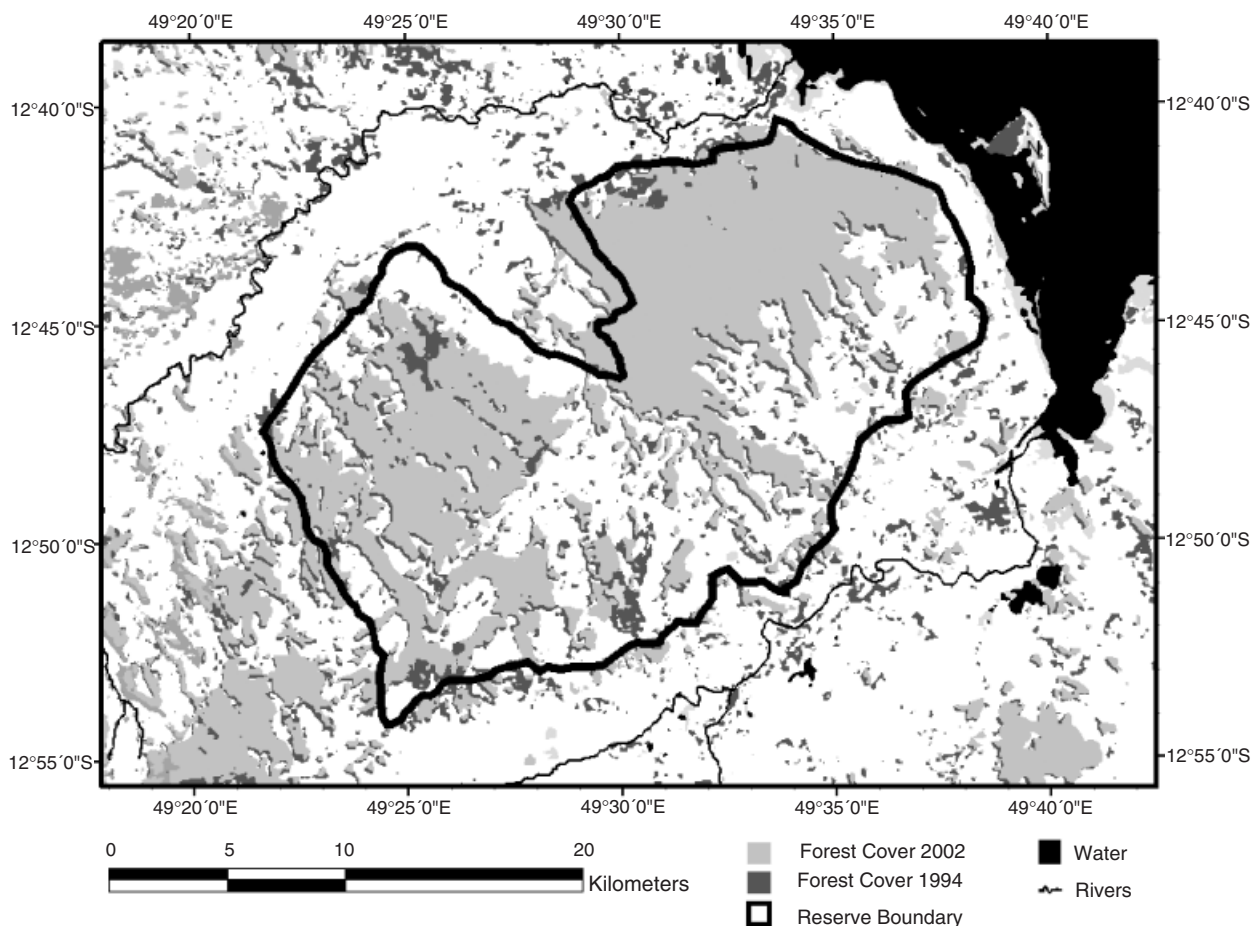
The highest encounter rate for primates was found at Anilotra (3.1 groups km<sup>-2</sup>). The two diurnal primate species that occur here (*E. coronatus* and *E. sanfordi*) were indifferent to the presence of observers. In contrast, encounter rates for primates at other sites visited within the Ankarana and Ambery forests were much lower (Table 3). The reactions of the two *Eulemur* species at these sites were characterized by immediate flight upon visual or auditory contact with humans (*E. coronatus*: 12 of 23 encounters; *E. sanfordi*: six of 6 encounters).

#### Available habitat and its decline

Available habitat within the geographic range reported for Perrier's sifaka comprised an area of 295.6 km<sup>2</sup>, with only 218.7 km<sup>2</sup> of this total occurring in the protected area of Analamerana. Forests falling within the boundaries of Ankarana were not included in our calculations because our surveys did not uncover the presence of Perrier's sifakas

**Table 3** Number of primate group sightings and encounter rates per km at rapid survey sites

Site name (number)	<i>Propithecus perrieri</i>		<i>Eulemur coronatus</i>		<i>Eulemur sanfordi</i>		<i>Hapalemur occidentalis</i>		Total primates Groups km <sup>-1</sup>
	# Groups	Groups km <sup>-1</sup>	# Groups	Groups/km	# Groups	Groups km <sup>-1</sup>	# Groups	Groups km <sup>-1</sup>	
Anilotra <sup>a</sup> (3)	0	0	28	1.68	24	1.49	0	0	3.11
Deuxieme Riviere <sup>a</sup> (4)	0	0	5	0.31	2	0.13	0	0	0.44
Sentier Botanique <sup>a</sup> (5)	0	0	11	0.52	4	0.19	0	0	0.70
Mahory <sup>a</sup> /Nosibe <sup>b</sup> (6)	0	0	5	0.35	2	0.13	0	0	0.49
Ambery <sup>b</sup> (7)	1	0.06	2	0.12	0	0	1	0.06	0.19

<sup>a</sup>Located within Ankarana.<sup>b</sup>Located outside Ankarana.**Figure 2** Forest cover changes at Analamerana.

there. Findings from our spatial analysis of forest coverage indicate losses of 23.2 km<sup>2</sup> (9.6%) of the total forested area within Analamerana during the period from 1994 to 2002 (Fig. 2). This generates an annual deforestation rate of 2.8 km<sup>2</sup> (1.2%) over the same period.

### Estimated population size

When the density of 3.1 individuals km<sup>-2</sup> is projected over the 295.6 km<sup>2</sup> forest area calculated as available habitat for Perrier's sifakas, an estimate of 915 remaining individuals is reached. When considered relative to existing reserve boundaries, this result suggests that some 240 individuals or 26% of

the total estimated population may be found in unprotected areas. Of these unprotected areas, 32% are represented by forest blocks of less than 1 km<sup>2</sup>. Finally, using the rule of thumb introduced earlier, we estimate the 'effective population size' of Perrier's sifakas at 230 individuals.

## Discussion

### Perrier's sifaka density and distribution

Our studies indicate that Perrier's sifakas are found at low densities throughout their range (3.1 individuals km<sup>-2</sup>). Meyers & Ratsirarson (1989) arrived at much higher density

estimates (20 individuals km<sup>-2</sup>) for Perrier's sifakas, but this discrepancy may be due to differing methodologies. The study of Meyers & Ratsiraron (1989) took place during the middle of the dry season and sampled preferentially along river banks. They also used a strip width that is only half that calculated for the current study. Furthermore, the area of detection, used to calculate survey area, was estimated based on subjective criteria and not by examining the distribution of sighting distances as has been recommended for primates (Brockelman & Ali 1987). Certainly these differences invite the possibility for arriving at a density estimate that is inflated by a factor of at least two. Furthermore, even earlier survey work (Petter *et al.*, 1977) produced density estimates comparable to those generated by the current study (see Table 1).

Both habitat disturbance (Skorupa, 1987; Ganzhorn, 1995) and hunting pressure (Peres, 1997) have been implicated in influencing the response of primates to observers. In particular, cryptic behaviour and reduced calling rates have been recorded in disturbed areas (Johns, 1985). The large proportion of primate sightings recorded in disturbed forest (i.e. 45% of all encounters) and the incidence of flight, which is a likely indication of hunting pressure, leaves open the possibility that our densities have been underestimated. However, unlike the two *Eulemur* species encountered, Perrier's sifaka was never observed to freeze during sighting events. This finding suggests that Perrier's sifakas might be more easily detected than the other primates encountered during our surveys (Johns, 1985). *Eulemur coronatus* and *E. sanfordi* have a pelage coloration that mixes well with the backdrop of deciduous forests at Analamerana and perhaps crypsis is a less effective strategy for avoiding humans for the conspicuous all-black Perrier's sifaka. Efforts to examine these possibilities and how they influence the detectability of different primate species at Analamerana should be incorporated into future surveys.

Our finding that the effective population size of Perrier's sifakas may not exceed 230 individuals may have serious consequences for the viability of the population. Due to the rate at which genetic variation is lost at population sizes of less than 500, some scholars (Franklin, 1980; Harcourt, 1995) have expressed concern over probabilities for long-term (i.e. hundreds of years) persistence. However, further analysis of the severity of this threat to *P. perrieri* requires more precise estimates of effective population size, which will need more detailed information on the breeding structure and life-history characteristics of this species (Lande & Barrowclough, 1987).

A considerable proportion of the estimated remaining population (i.e. 26%) may occur in unprotected forests. At one of the unprotected sites (i.e. Ambery), we found active fires and associated agricultural plots encroaching on the range of observed Perrier's sifaka groups. Furthermore, despite its remoteness and low human population density, Analamerana appears to receive regular traffic from immigrants travelling opportunistically into the gold-producing region of Daraina, located some 60 km to the south. Travellers have been encountered carrying slingshots, and indirect evidence of unauthorized visitors, such as holes excavated to search for sapphires, was sometimes apparent along our survey routes.

The absence of Perrier's sifakas from Ankarana may be another cause for concern because this species had been sighted there as recently as in the late 1980s (Hawkins *et al.*, 1990). However, the results from our surveys provide support for the argument that earlier sightings of Perrier's sifakas at Ankarana may have been representative of migrant animals and not of a resident population. At Ankarana, encounter rates for primates were high in only one of the four sites visited, Anilotra (Fig. 1: site 3). This site is frequented by tourists and researchers, a factor that has enhanced conservation efforts elsewhere in Madagascar (Wright & Andriamihaja, 2003). Furthermore, the reserve is monitored regularly by park officials to deter hunting and other illegal activities. Nevertheless, traces of the recent boom in sapphire discovery that began during the mid-1990s in Ankarana (Cardiff & Befourouack, 2003) were noticeable along major paths at Anilotra. Elsewhere within the reserve, primates were encountered at low rates and fled upon visual contact with observers, in stark contrast to conditions at Anilotra. Individuals from local communities bordering Ankarana confirmed the recent presence of illegal miners and emphasized the active hunting of *Eulemur* species.

The absence of Perrier's sifakas from Ankarana might also be rooted in factors surrounding its behavioural ecology. In particular, Meyers & Ratsiraron (1989) suggest that the microhabitat niche offered by riparian forests (a habitat lacking in Ankarana) might be required by Perrier's sifakas. Additionally, evidence from behavioural studies indicates that Perrier's sifakas come to the ground frequently to drink water from river beds (Mayor & Lehman, 1999). Indeed the majority of our encounters with Perrier's sifakas were located in close proximity to annually flowing streams (M. A. Banks, unpubl. data). Similarly, in other studies aimed at assessing the impact of seasonal water scarcity on the ranging patterns of lemurs, animals were found to centre their activity in the immediate proximity of water sources during the driest periods (Scholz & Kappeler, 2004; Gould, Sussman & Sauther, 1999). In the sites we visited at Ankarana water was extremely scarce and the only available water sources for primates during the dry season came from underground rivers. This difference between these parts of Ankarana and Analamerana may help to explain the absence of the Perrier's sifaka here, particularly during the driest parts of the year when our surveys were conducted. Future primate surveys at Ankarana should include sites supporting permanent waterways to explore the possibility that *P. perrieri* incidence is driven by the availability of water sources.

Our single encounter with a group of *H. occidentalis* during transect walks at Ambery may be a useful step towards assessing the population status of this species, because there have been few studies where the local population levels of this species have been estimated from survey methods. Our failure to detect this species at both Ankarana and Analamerana, despite its anticipated presence there (see Mittermeier *et al.*, 2006a), suggests that additional survey work will be necessary to better determine the status of this species within both reserves. The two *Eulemur* species (*E. coronatus* and *E. sanfordi*) were found in nearly all of

the sites visited, yet both species were found at much lower densities and abundances than reported in both humid and dry forests elsewhere (Mittermeier *et al.*, 2006a; Garbutt, 1999). The ranges of these two *Eulemur* species are restricted to northern Madagascar (Mittermeier *et al.*, 2006a) and the only protected areas where these species occur are Analamerana, Ankarana, the Montagne d'Ambre National Park and the Forêt d'Ambre Special Reserve. In the light of these findings, revisions surrounding the conservation status of these primate species may be warranted.

Results from our spatial analysis indicate that forests within Analamerana have decreased in area by nearly 10% in an 8-year-period. Given the remoteness and size of the reserve, monitoring Analamerana and its surrounding areas is sure to remain a daunting task for the region's undermanned park service. In unprotected forests that continue to support the Perrier's sifakas, forest loss may be even higher. Clearly habitat decline remains a major obstacle for conservation managers working in this part of Madagascar (Smith, 1997). Resource limitations for conservation, persistent threats on lemur populations in general, as well as the low population density and limited distribution of high profile taxa such as the Perrier's sifaka suggest that conservation managers are facing substantial challenges to safeguard the natural environment in this unique and important part of Madagascar.

### Management recommendations

1. Forests falling in between Ankarana and Analamerana should be annexed for inclusion as part of these protected areas, because these localities support Perrier's sifakas and other threatened primates.
2. Encounter rates for primates occupying areas that regularly receive tourists and researchers are higher than in areas without them, suggesting that the enhancement of infrastructure at Ankarana and Analamerana to support moderate tourist volumes and research presence should be considered.
3. Research aimed at uncovering relationships between Perrier's sifaka abundance and habitat conditions should become a focus of future fieldwork because insights into some of these patterns would help to build upon the current study, providing a more refined estimate of current population size and enabling conservation efforts to target the most important habitats.

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### References

- Baillie, J.E.M., Hilton-Taylor, C. & Stuart, S.N. (2004). *2004 Red List of threatened speciesTM: a global species assessment*. Gland, Switzerland: IUCN.
- Borries, C., Larney, E., Kreetiyutanont, K. & Koenig, A. (2002). The diurnal primate community in a dry evergreen forest in Phu Khieo Wildlife Sanctuary, north-east Thailand. *Nat. Hist. Bull. Siam Soc.* **50**, 75–88.
- Brockelman, W.Y. & Ali, R. (1987). Methods of surveying and sampling forest: primate populations. In *Primate conservation in the Tropical Rain Forest*: 23–62. Marsh, C.W. & Mittermeier, R.A. (Eds). Alan R. Liss, Inc.: New York.
- Buckland, S.T., Anderson, D.R., Burnham, K.P. & Laake, J.L. (1993). *Distance sampling: estimating abundance of biological populations*. London: Chapman & Hall.
- Cardiff, S. & Befourouack, J. (2003). The reserve speciale d'Ankarana. In *The natural history of Madagascar: 1501–1507*. Goodman, S.M. & Benstead, J.P. (Eds). Chicago: University Chicago Press.
- Cowlshaw, G. & Dunbar, R.I.M. (2000). *Primate conservation biology*. Chicago: University of Chicago Press.
- Dufils, J.M. (2003). Remaining forest cover. In *The natural history of Madagascar*: 88–96. Goodman, S.M. & Benstead, J.P. (Eds). Chicago: University Chicago Press.
- Fashing, P.J. & Cords, M. (2000). Diurnal primate densities and biomass in the Kakamega Forest: an evaluation of census methods and a comparison with other forests. *Am. J. Primate.* **50**, 139–152.
- Franklin, I.R. (1980). Evolutionary change in small populations. In *Conservation biology: an evolutionary-ecological perspective*: 135–149. Soulé, M.E. & Wilcox, B.A. (Eds). Sunderland, Massachusetts: Sinauer Associates, Inc.
- Ganzhorn, J.U. (1995). Low-level forest disturbance effects on primary production, leaf chemistry, and lemur populations. *Ecology* **76**, 2084–2096.
- Ganzhorn, J.U., Lowry, P.P., Schatz, G.E. & 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., Malcomber, S., Andrianantoanina, O. & Goodman, S.M. (1997). Habitat characteristics and lemur species richness in Madagascar. *Biotropica* **29**, 331–343.
- Garbutt, N. (1999). *Mammals of Madagascar*. Sussex: Pica Press.

- Gould, L., Sussman, R. & Sauther, M. (1999). Natural disasters and primate populations: the effects of 2-year drought on a naturally occurring population of ring-tailed lemurs (*Lemur catta*) in south-western Madagascar. *Int. J. Primatol.* **20**, 69–84.
- Green, G.M. & Sussman, R.W. (1990). Deforestation history of the eastern rain forests of Madagascar from satellite images. *Science* **248**, 212–215.
- Harcourt, A.H. (1995). Population viability estimates - theory and practice for a wild gorilla population. *Conserv. Biol.* **9**, 134–142.
- Hawkins, A.F.A., Chapman, P., Ganzhorn, J.U., Bloxam, Q.M.C., Barlow, S.C. & Tonge, S.J. (1990). Vertebrate conservation in Ankarana special reserve, northern Madagascar. *Biol. Conserv.* **54**, 83–110.
- Irwin, M.T., Johnson, S.E. & Wright, P.C. (2005). The state of lemur conservation in south-eastern Madagascar: population and habitat assessments for diurnal and cathemeral lemurs using surveys, satellite imagery and GIS. *Oryx* **39**, 204–218.
- Jernvall, J. & Wright, P.C. (1998). Diversity components of impending primate extinctions. *Proc. Nat. Acad. Sci. USA* **95**, 11279–11283.
- Johns, A.D. (1985). Differential detectability of primates between primary and selectively logged habitats and implications for population surveys. *Am. J. Primatol.* **8**, 31–36.
- Johnson, S.E. & Overdorff, D.J. (1999). Survey of brown lemurs (*Eulemur fulvus* spp.) in south-eastern Madagascar: methods-testing and conservation implications. *Am. J. Primatol.* **47**, 51–60.
- Lande, R. & Barrowclough, F. (1987). Effective population size, genetic variation, and their use in population management. In *Viable populations for conservation: 87–123*. Soule, M. (Ed.). Cambridge, UK: Cambridge University Press.
- Lehman, S.M. & Mayor, M. (2004). Dietary patterns in Perrier's sifakas (*Propithecus diadema perrieri*): a preliminary study. *Am. J. Primatol.* **62**, 115–122.
- Lehman, S.M., Mayor, M. & Wright, P.C. (2005). Ecogeographic size variations in sifakas: a test of the resource seasonality and resource quality hypothesis. *Am. J. Phys. Anthropol.* **126**, 318–328.
- Le Normand, B. (1988). Repartition de *Propithecus diadema perrieri*. In *L'Equilibre des Ecosystemes Forestiers à Madagascar: 95*. Rakotovo, L., Barre, V. & Sayer, J. (Eds). Gland, Switzerland & Cambridge, UK: IUCN.
- Martin, P. & Bateson, P.P.G. (1993). *Measuring behaviour: an introductory guide*. Cambridge: Cambridge University Press.
- Mayor, M. & Lehman, S.M. (1999). Conservation of Perrier's sifaka (*Propithecus diadema perrieri*) in Analamera Special Reserve, Madagascar. *Lemur News* **4**, 21–23.
- Mayor, M.I., Sommer, J.A., Houck, M.L., Zaonarivelo, J.R., Wright, P.C., Ingram, C., Engel, S.R. & Louis, E.E. (2004). Specific status of *Propithecus* spp. *Int. J. Primatol.* **25**, 875–900.
- Meyers, D.M. & Ratsirarson, J. (1989). Distribution and conservation of two endangered sifakas in northern Madagascar. *Primate Conserv.* **10**, 81–86.
- Mittermeier, R.A., Konstant, W.R., Hawkins, F., Louis, E.E., Langrand, O., Ratsimbazafy, J., Rasoloarison, R., Ganzhorn, J.U., Rajaobelina, S., Tattersall, I. & Meyers, D.M. (2006a). *Lemurs of Madagascar*. 2nd edn. Columbia: Conservation International.
- Mittermeier, R.A., Konstant, W.R. & Rylands, A.B. (2003). Lemur conservation. In *The natural history of Madagascar: 1538–1543*. Goodman, S.M. & Benstead, J.P. (Eds). Chicago: University Chicago Press.
- Mittermeier, R.A., Valladares-Pádua, C., Rylands, A.B., Eudey, A.A., Butynski, T.M., Ganzhorn, J.U., Kormos, R., Aguiar, J.M. & Walker, S. (2006b). Primates in peril: the world's 25 most endangered primates, 2004–2006. *Primate Conserv.* **20**, 1–28.
- Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B. & Kent, J. (2000). Biodiversity hotspots for conservation priorities. *Nature* **403**, 853–858.
- National Research Council (1981). *Techniques for the study of primate population ecology*. Washington, DC: National Academy Press.
- Nelson, R. & Horning, N. (1993). AVHRR-lac estimates of forest area in Madagascar, 1990. *Int. J. Remote Sensing* **14**, 1463–1475.
- Peres, C.A. (1997). Effects of habitat quality and hunting pressure on arboreal folivore densities in neotropical forests: a case study of howler monkeys (*Alouatta* spp). *Folia Primatol.* **68**, 199–222.
- Petter, J.J., Albignac, R. & Rumpler, Y. (1977). *Lemurine mammals (Primates, Prosimians)*. Faune de Madagascar. Paris: ORSTROM.
- Scholz, F. & Kappeler, P.M. (2004). Effects of seasonal water scarcity on the ranging behavior of *Eulemur fulvus rufus*. *Int. J. Primatol.* **25**, 599–613.
- Skorupa, J.P. (1987). Do line-transect surveys systematically underestimate primate densities in logged forests? *Am. J. Primatol.* **13**, 1–9.
- Smith, A.P. (1997). Deforestation, fragmentation, and reserve design in western Madagascar. In *Tropical forest remnants: ecology, management, and conservation of fragmented communities: 415–41*. Laurance, W.F. & Bierregaard, R.O.W. Jr. (Eds). Chicago: University of Chicago Press.
- Whitesides, G.H., Oates, J.F., Green, S.M. & Kluberanz, R.P. (1988). Estimating primate densities from transects in a West-African rain-forest – a comparison of techniques. *J. Anim. Ecol.* **57**, 345–367.
- Wright, P.C. & Andriamihaja, B. (2003). The conservation value of long-term research: a case study from the Parc National de Ranomafana. In *The natural history of Madagascar: 1485–1488*. Goodman, S.M. & Benstead, J.P. (Eds). Chicago: University Chicago Press.
- Wright, P.C. & Jernvall, J. (1999). The future of primate communities: a reflection of the present? In *Primate communities: 295–310*. Fleagle, J.F., Janson, C. & Reed, K.A. (Eds). Cambridge: Cambridge University Press.