

Conservation Status and Abundance of the Crowned Sifaka (*Propithecus coronatus*)

Authors: Salmona, Jordi, Rasolondraibe, Emmanuel, Jan, Fabien, Besolo, Aubin, Rakotoarisoa, Heriniaina, et al.

Source: Primate Conservation, 2014(28) : 73-83

Published By: Conservation International

URL: <https://doi.org/10.1896/052.028.0122>

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Conservation Status and Abundance of the Crowned Sifaka (*Propithecus coronatus*)

Jordi Salmona¹, Emmanuel Rasolondraibe², Fabien Jan¹, Aubin Besolo², Heriniaina Rakotoarisoa², Sam Viana Meyler¹, Sébastien Wohlhauser³, Clément Rabarivola⁴ and Lounès Chikhi^{1,5,6}

¹Instituto Gulbenkian de Ciencia, Oeiras, Portugal

²Cité Universitaire, Université de Mahajanga, Campus Universitaire Ambondrona, Mahajanga, Madagascar

³Fanamby NGO, Ankadivato, Antananarivo, Madagascar

⁴Faculté des Sciences, Université de Mahajanga, Campus Universitaire Ambondrona, Mahajanga, Madagascar

⁵CNRS, Laboratoire Evolution & Diversité Biologique, Université Paul Sabatier, Toulouse, France

⁶Université de Toulouse, Toulouse, France

Abstract: The crowned sifaka (*Propithecus coronatus*) is Endangered. It has a large but highly fragmented distribution; its known range extends from the Betsiboka River in the north of Madagascar, to the Mahavavy River in the north-west, and down to the Tsiribihina River in the south-west. The species lives in forest habitats that are highly and increasingly fragmented and are continuously suffering perturbations and destruction. In order to carry out effective conservation measures targeting *P. coronatus*, its conservation status needs to be updated so that measures can be taken before anthropogenic or natural environmental changes lead to the extirpation of the species in most of its forests. We (i) identified forest fragments where the species is still present and (ii) using the line-transect “Distance” sampling method, estimated the population size and density in the principal remaining forest fragments in the northern part of its range, including both protected and unprotected areas. We visited most of the forests in the northern part of its range in order to update the current area of occupancy, and to rate the state of its forests using a qualitative “forest quality index.” Our survey results have shown that (i) a large number of forests have disappeared or decreased in size in the last 10 years, and (ii) population densities vary considerably among forest fragments (ranging from 49 to 309 individuals per km²), with some very high densities in forests located along the Mahavavy River and in the Antrema area. Their abundance in the area surveyed is likely to be between 4,226 and 36,672 individuals, and most probably above 10,000. It is difficult to extrapolate from these estimates to the total abundance across the species’ entire range, but we estimate that it is likely to be large, probably between 130,000 and 220,000 individuals. Unfortunately, many field observations suggest that its populations continue to decline at a high rate due to habitat loss and hunting, and we argue for the re-evaluation of the conservation status from Endangered A2cd to Endangered A4acd, and the need to survey the rest of the range of *P. coronatus*.

Key Words: Population density, Distance sampling, *Propithecus coronatus*, conservation status, area of occupancy

Introduction

Crowned sifakas (*Propithecus coronatus*) are diurnal lemurs, inhabiting mainly dry deciduous forests and mangroves (Petter and Andriatsarafa 1987). Neither the distribution of *P. coronatus* nor its total population size are well known (Mittermeier *et al.* 2010). Its distribution was first shown to encompass the north-west of Madagascar between the Betsiboka (which separates it from Coquerel’s sifaka *Pwcoquereli*) and Mahavavy (where it is believed to hybridize with Decken’s sifaka, *P. deckenii*) rivers (Kaudern 1915). Nevertheless, early work from the 1929–1931 Archbold Expedition reported the presence of melanistic individuals

in the Bongolava population of *P. deckenii* (Tattersall 1986), which might be attributed to *P. coronatus*, and Paulian (1953) also reported the presence of *P. coronatus* near Tsiroanomanididy, south of the Manambolo River (in Wilmé *et al.* 2006). Later, Petter and Andriatsarafa (1987) reported the past presence of *P. coronatus* further to the east, in the Ambohitantely Special Reserve, but this record may have arisen from an error in translation (Rakotonirina *et al.* this issue) leaving unresolved its past presence in the region east of the Ikopa River (Rakotonirina *et al.* this issue). Thalmann and Rakotoarison (1994) reported its occurrence to the south of the Manambolo River (south of the putative distribution of *P. deckenii*). All these studies thus suggested that *P. coronatus* might have

a distribution much larger than was previously thought. In particular, these authors proposed for the first time a geographic range that would include the inter-river systems (IRS) between the Betsiboka and Mahavavy rivers in the north-west (corresponding to IRS1 and IRS4 in Fig. 1) and between the Manambolo and Tsiribihina rivers in the central-west. This

distribution would thus surround that of *P. deckenii*, which would then be restricted to the IRS2 and IRS3 areas (Fig. 1) with some contact zones along the main rivers and in the Bongolava region. This hypothetical geographic range has not yet been entirely validated because of the remoteness of these regions, and problems of security when visiting them.

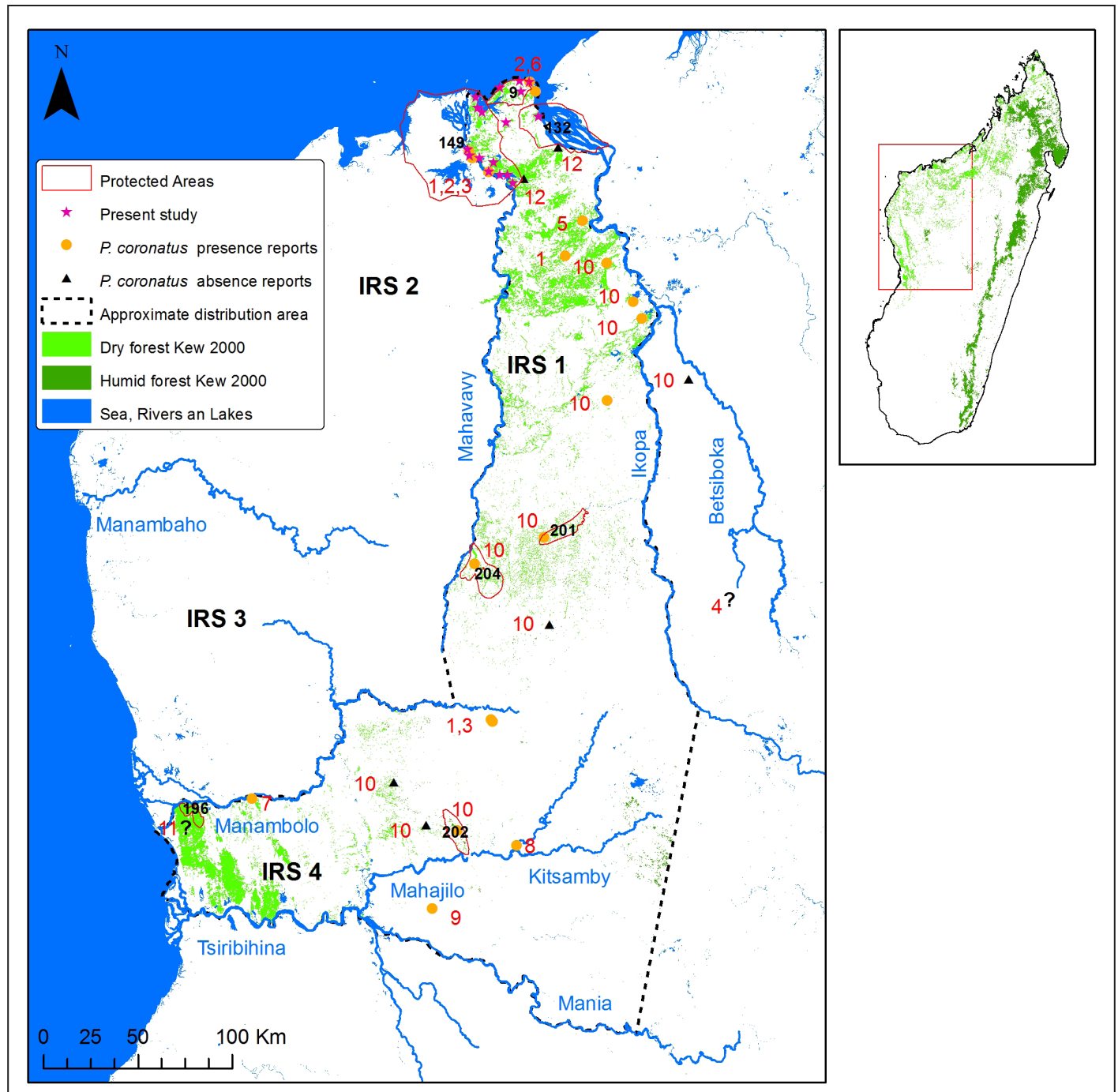


Figure 1. Map of the estimated area of occupancy of *P. coronatus*. This map shows the localities for *P. coronatus* in the literature and the probable distribution of the species. The references used to build this map are indicated by the red numbers whereas the corresponding orange dots identify the location where sifakas were observed. The black numbers correspond to protected areas. IRS (Inter-River System) 1 to 4 are based on Thalmann and Rakotoarison (1994). Reports of absence are based on rapid surveys and should not be taken at face value. Forests outside of the range of *P. coronatus* are not shown.

Reports of the presence of *P. coronatus* (red numbers): 1: Wilmé *et al.* (2006); 2: Curtis *et al.* (1998); 3: Thalmann *et al.* (2002); 4: Petter and Andriatsafara (1987); 5: Rasoloharijaona *et al.* (2005); 6: Müller *et al.* (2000); 7: Thalmann and Rakotoarison (1994a); 8: Tattersall (1986); 9: Razafindramanana and Rasamimanana (2010); 10: Rakotonirina *et al.* (this issue); 11: Report of *P. verreauxi*, Zicoma (1998) in Wilmé *et al.* (2006); 12: This study (reports of absence).

Protected areas (black numbers): 9: SFUM d'Antrema APT; 132: Bombetoka-Belemboka NAP; 149: Complexes Zones Humides Mahavavy-Kinkony APT; 196: Site Ambondrobe NAP; 201: Forêt d'Ambohitromby SP; 202: Forêt d'Andasilaitaka SP; 204: Forêt de Mahajoby SP.

Razafindramanana and Rasamimanana (2010) extended the species' range in Dabolava and Miandrivazo, to the south of the Mahajilo River, suggesting as a result that the Mania River should be the northern limit of *P. verreauxi* and should correspond to the extreme southern limit of *P. coronatus*. This supported the suggestions of Thalmann and Rakotoarison (1994) and Wilmé and Callmander (2006). Finally Rakotonirina *et al.* (this issue) recently conducted a widespread survey and confirmed the presence of *P. coronatus* to the west of the Ikopa River and to the north of the Mahajilo River, again confirming previous hypotheses concerning its range limits.

While most presence-absence studies of *P. coronatus* have been carried out in the north-west (Curtis *et al.* 1998; Müller *et al.* 2000 in Katsepy, Anjamena, and Anaborengy), it should be noted that some fragments of the southern area of the IRS1, for example, Andranovelona/Madirovalo (Rasoloharijaona *et al.* 2005), Madirolavo (change to: Sussman 1977 in Wilmé *et al.* 2006) have been visited. Most of the forest fragments of this extended and putative geographic range, however, have not yet been surveyed (Fig. 1), and only a few studies have been carried out to estimate *P. coronatus* population densities. Moreover, these studies have produced very different figures.

To our knowledge, three studies have estimated *P. coronatus* densities in Anjamena. Müller (1997) estimated a very high density of 543 ind/km², based on home range size. Curtis *et al.* (1998) reported density estimates of 32 ind/km² (a value 17 times smaller than that of Müller 1997), whereas Müller *et al.* (2000) reported densities of 173 ind/km². In Katsepy, Curtis *et al.* (1998) found densities of 5 ind/km², whereas Pichon *et al.* (2010), using long-term survey data, estimated a minimum of 300 ind/km² in the Badrala forest of the Antrema Forest Station close to Katsepy.

Due to their matriarchal social system, with groups usually composed of two to eight individuals, and their relatively long generation time (probably between 6 and 15 years, based on data from *Propithecus verreauxi*; Richard *et al.* 2002; Lawler *et al.* 2007), the recovery of small isolated populations is likely to be difficult both from a demographic and genetic point of view. The lack of consistent density estimates, together with the limited number of studies and regions surveyed, and the huge threats imposed on primates and sifakas across Madagascar, led to the classification of *P. coronatus* as Critically Endangered in 1996 (Baillie and Groombridge 1996, in IUCN 2008). Its status was updated in 2008 and considered Endangered A2cd (IUCN 2008) as it was thought to have undergone a reduction of more than 50% over the past three generations or 30 years (assuming a generation length of 10 years), due primarily to a decline in area and quality of habitat within its known range, but also due to hunting. Its status as Endangered was reaffirmed in a Red Listing Workshop held in Antananarivo, Madagascar, in 2012.

In this study, we collected presence-absence survey results for 70 forest fragments and 12 corridors and gallery forests around 19 sites in the north-west of the Betsiboka-Mahavavy IRS. Furthermore, we provide here new density

estimates of *P. coronatus* for six localities. Using density and available GIS data on forest cover, we estimated the area of occupancy and the total population size of the species. Finally, we discuss a possible update to the conservation status of *P. coronatus*.

Methods

Presence-absence survey and human impact assessment

To detect the presence of *P. coronatus* and compute a "quality index" of the forest fragments in the northern part of its range, we visited 70 forest fragments and 12 forest corridors, in the vicinities of 19 sites (villages or chief towns) between the Betsiboka and Mahavavy rivers during two field seasons: from July to October 2009, and April to July 2010 (Table 1; Fig. 2).

The first surveys were in three protected areas. We surveyed the forests neighboring the Kingany, Boeny Ampasy, Boeny Aranta, Antsilaiza, Anaborengy, Ambohibary, Antanimalandy and Ankarahara localities in the Mahavavy-Kinkony complex managed by the Malagasy NGO Asity. The forests around Kingany and Boeny Ampasy are mainly small, dry semi-deciduous, forest fragments. The forest fragments surrounding the Mataitromby locality are in the Bombetoka-Belemboka protected area managed by the Malagasy NGO Fanamby. Forests visited around Antrema, Katsepy, Masokohamena and Ambanjabe are in the Antrema Forest Station protected area, which contains three of the typical north-western ecosystems (dry semi-deciduous forest, mangrove swamp, savanna), which suffer moderate anthropogenic pressure. We also visited unprotected forest fragments around Androhibe, Ankarabato and Antsalatsala.

In each survey site, we walked slowly and quietly in the forests or on its edges in order to detect the presence of *P. coronatus*. When a group of sifaka was found, its size and composition was estimated and GPS coordinates were recorded. The general human impact on the forest was estimated qualitatively: fire residues, logging, evidence of poaching, forest clearing and charcoal ovens were registered when observed.

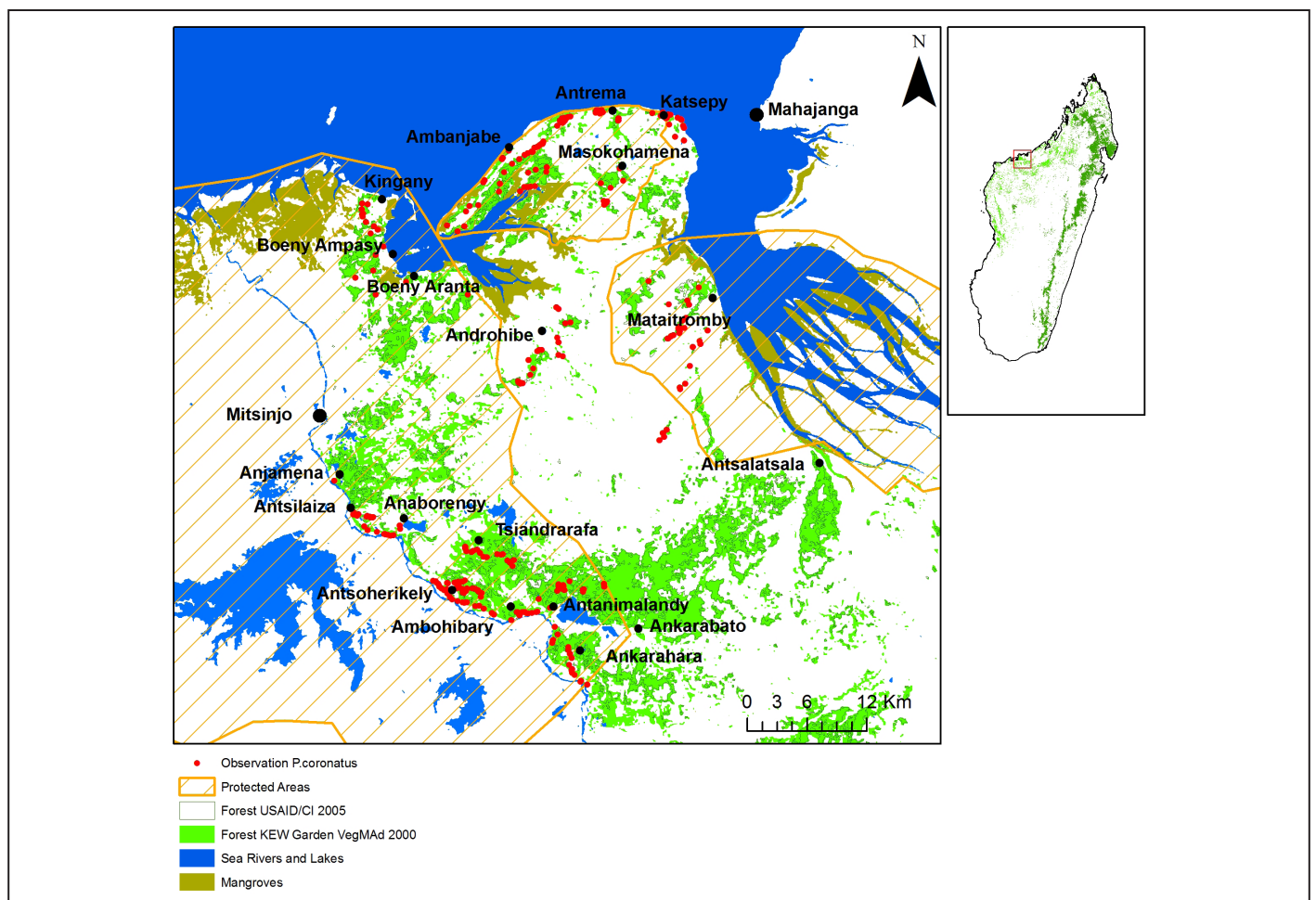
Population densities and total species abundance

To study variation in the density of *P. coronatus* among forest patches, we carried out line transect sampling surveys, following the distance sampling methodology (Peres 1999; Buckland *et al.* 2001), in six of the principal forest fragments in the northern part of its range: Ambohibary, Antsilaiza, Antsoherikely, Antanimalandy, Ankarahara, located along the Mahavavy River (Fig. 2); and Antrema in the north along the Mozambique Channel. The selection of these forests was motivated mainly by their size and characteristics, on the basis that distance sampling methods require a minimum number of observations to provide reliable estimates. Density surveys were thus not performed in small fragments and corridors. All were of lowland dry semi-deciduous forest, and suffered different levels of human disturbance.

Table 1. Coordinates, characteristics and number of visited forests during crowned sifaka surveys.

Site (closest village or chief town)	Region	Department	Commune	GPS NS	GPS EW	No. of visited forest fragment	No. of visited corridor	Forest type*
Ambanjabe	Boeny	Mitsinjo	Katsepy	-15.743	46.069	9		1-4,8,9
Ambohibary	Boeny	Mitsinjo	Ankarabato	-16.160	46.070	1		3,4,7,8
Anaborengy	Boeny	Mitsinjo	Mitsinjo	-16.080	45.970	1		3,4,7,8
Androhibe	Boeny	Mitsinjo	Antongomena-Bevary	-15.910	46.100	2	3	3-6,8,9
Anjamena	Boeny	Mitsinjo	Mitsinjo	-16.040	45.910	5		3,4,7,8
Ankarabato	Boeny	Mitsinjo	Ankarabato	-16.180	46.190	3		3-6,8,9
Ankarahara	Boeny	Mitsinjo	Ankarabato	-16.200	46.135	1		3,4,7,8
Antanimalandy	Boeny	Mitsinjo	Ankarabato	-16.160	46.110	2		3,4,7,8
Antrema	Boeny	Mitsinjo	Katsepy	-15.710	46.166	3		1-4,8,9
Antsalatsala	Boeny	Marovoy	Behamarivo	-16.030	46.360	3	1	3-6,9
Antsilaiza	Boeny	Mitsinjo	Mitsinjo	-16.070	45.920	6	3	3,4,7,8
Antsoherikely	Boeny	Mitsinjo	Ankarabato	-16.145	46.015	2		3,4,7,8
Boeny Ampasy	Boeny	Mitsinjo	Antongomena-Bevary	-15.840	45.960	4		3-6,8,9
Boeny Aranta	Boeny	Mitsinjo	Antongomena-Bevary	-15.860	45.980	9		3-6,8,9
Katsepy	Boeny	Mitsinjo	Katsepy	-15.714	46.214	6		3-6,8,9
Kingany	Boeny	Mitsinjo	Antongomena-Bevary	-15.790	45.950	3		1-4,8,9
Mataitromby	Boeny	Mitsinjo	Ankarabato	-15.880	46.260	6	5	3-6,8,9
Mazokohamena	Boeny	Mitsinjo	Katsepy	-15.760	46.175	3		3-6,8,9
Tsiandrara	Boeny	Mitsinjo	Ankarabato	-16.100	46.040	1		3-6,8,9
Total						70	12	

*1: mangroves; 2: littoral forest; 3: Dry primary forest; 4: Dry secondary forest; 5: Corridor forest along canyon and rivers; 6: recently burnt and regenerating forest; 7: high canopy; 8: middle size canopy; 9: low canopy

**Figure 2.** Map of the survey sites. The locations visited during our surveys with details regarding the presence of crowned sifakas. Forests outside of the range of *P. coronatus* are not shown.

Our census took place during the dry season; from July to October 2009 (four months) and April to July 2010 (four months). Between three and five line-transects were randomly delineated at each site; 20 line-transects in total. GPS coordinates were recorded every 20 m along each transect. The transects ranged from 800 m to 3,500 m in length. They were surveyed 6–10 times during 3–5 days by three 2-member teams, to achieve at least 40 observations, as recommended by Peres (1999). Every day, one team member changed teams and transects to avoid observational biases among teams and to ensure that at least one team member had already walked that transect (Quéméré *et al.* 2010).

On seeing a sifaka group we collected the following data: date, time, transect number, group size, group spread, and sighting distance and angle to the center of the group (to compute perpendicular sighting distance). We then estimated sifaka densities (ind/km²) in each fragment using the DISTANCE 6.0 software (Thomas *et al.* 2010). In this method, the surveyed area corresponded to the product of the total survey effort per fragment (km) and the effective sighting width (ESW). The ESW is estimated using a calculation of the decreasing probability of seeing an animal as a function of its distance from the transect. Various functions can be used to model this probability and estimate ESW. Here we tested the uniform, hazard rate, and half normal models with cosine, polynomial and Hermite adjustments and compared them using the Akaike Information Criterion (AIC) as recommended by Buckland *et al.* (2001).

The global *P. coronatus* distribution was determined using all available *P. coronatus* observations (Sussman 1977; Tattersall 1986; Petter and Andriatsarafana 1987; Thalmann and Rakotoarison 1994; Curtis *et al.* 1998; Müller *et al.* 2000; Thalmann *et al.* 2002; Rasoloharijaona *et al.* 2005; Wilmé *et al.* 2006; Razafindramanana and Rasamimanana 2010; Rakotonirina *et al.* this issue). Combined, the published data argue for a wide-ranging distribution of the species delimited by the Betsiboka and Ikopa rivers in the east, by the Mahavavy and Manambolo rivers in the west, and by the Tsiribihina and Mania rivers in the south (Fig. 1). Its occurrence between the Mahavavy and the Manambolo, and between the Mania and the Ikopa rivers has been defined approximately, without clear observational data, and needs thus to be confirmed. Melanistic variants of *P. deckenii* in Ambohijanahary and Kasijy have not been taken into account to delimit the probable range of *P. coronatus* (see Rakotonirina *et al.* this issue). As the report of the past presence of crowned sifaka in Ambohitantely now appears to have been a translation error (Rakotonirina *et al.* this issue), and as these authors (this issue) reported their absence in Bekirobo, the area between the Ikopa and the Betsiboka rivers was not included. The extent of suitable habitat across the range of *P. coronatus* was calculated using forest classification from the Madagascar Vegetation Mapping Project data (available online at <http://www.kew.org/gis/projects/mad_veg/datasets.html>; Moat and Smith 2007) from 1999 and 2000 satellite images, and MEFT-USAID-CI (2009) from 2005 satellite images classification on ArcMap

software (ESRI). To estimate the total species abundance, we multiplied the minimum and average density estimates by the area of occupancy, which was obtained using the two different GIS (Geographic Information System) data sets (Moat and Smith 2007; MEFT-USAID-CI 2009).

Results

Species presence-absence

In all, 331 discrete social groups were sighted during the presence-absence surveys. They comprised a total of 1,234 individuals (adults only) with an average group size of 3.6 (Table 2) during a 169 day × people survey effort. Ninety-eight groups had newborn offspring (29.6% of the groups seen). Sifakas were not found in the forest fragment surrounding the village of Anaborengy, and around localities in the south-east of the survey area, from Ankarabato to Antsalatsala. Time spent in the latter area was short but this is known to be a “Dahalo” (Zebu thief) area and most of the forests were burned or burning during our visit (August 2010). Few observations were made in Anjamena and in the Boeny-Kingany region. Most forests had been cleared around Anjamena, and we therefore spent little time in this area. The Boeny-Kingany region is composed of small and highly fragmented forests. Most of those neighboring Boeny Ampasy had been burned a few years before, and the sifaka encounter rate in the regenerating fragments was lower than one group per day. To our surprise, we found large numbers of sifaka groups in the Mataitromby and Androhibe forest corridors along small rivers located between the Betsiboka and Mahavavy rivers.

Population density and size

We surveyed a total of 220 km and made 444 sightings of social groups comprising 1,753 individuals (note that these numbers do not always correspond to distinct groups or individuals, as each transect was repeated more than once). In agreement with surveys elsewhere (Plumptre and Reynolds 1994) including those for golden-crowned sifakas (*Propithecus tattersalli*) (Quéméré *et al.* 2010), the hazard-rate model was identified as the best fit for our data in all fragments. We gathered enough observations to accurately compute density estimates for five of the six survey sites (Table 3). Only 21 social groups (71 individuals) were observed in Antanimandry despite four days of census and a total of 12.71 km of survey effort. This limited number of observations (as a comparison, 156 groups corresponding to 281 individuals were observed in Antsoherikely in 2009 for 52.13 km surveyed, i.e., twice as many per km) did not allow us to accurately compute the ESW (Buckland *et al.* 2001). Nevertheless, we provide an estimate of sifaka density using the ESW estimated by Distance on the basis that the ESW estimates were unlikely to be much greater or smaller than for other sites. Results for Antanimandry should, however, be regarded with caution; indeed confidence intervals for this forest are very large (9–714) and little informative. Density estimates in all fragments range from 46 ind/km² in Ankarahara to 255 ind/km² in

Table 2. *Propithecus coronatus* presence-absence survey results and main threats observed.

Site	Year	a: Survey effort (days)	b: No. of people involved	Survey effort (a × b)	Observed number			Mean group size	Clearing for agriculture	Clearing for charcoal	Hunting evidence	Burnt forest
					Groups	Ind.	Infants					
Ambanjabe	2010	2	9	18	19	79	2	4.2	Yes	Yes		
Ambohibary	2009	4	1	4	14	53	6	3.8	Yes		Yes	
Anaborengy	2010	1	2	2	0	0	0	-	Yes			
Androhibe	2010	2	2	4	21	60	0	3.0	Yes			
Anjamena	2010	1	5	5	16	60	0	3.8	Yes		Yes	
Ankarabato	2010	1	3	3	0	0	0	-	Yes			Yes
Ankarahara	2009	5	1	5	17	60	9	3.5			Yes	
Antanimalandy	2009	5	2	10	8	24	3	3.2	Yes		Yes	
Antrema	2010	6	3	18	68	292	23	4.3		Yes		
Antsalatsala	2010	1	3	3	0	0	0	-	Yes	Yes		Yes
Antsilaiza	2010	4	6	24	26	120	0	4.6	Yes			
Antsoherikely	2009–2010	8	2	16	48	168	20	3.6	Yes		Yes	
Boeny Ampasy	2010	1	4	4	5	9	0	3.0		Yes		Yes
Boeny Aranta	2010	1	9	9	4	12	0	3.0		Yes		Yes
Katsepy	2009	2	4	8	13	41	5	3.4			Yes	Yes
Kingany	2010	2	3	6	14	62	0	4.4				Yes
Mataitromby	2009	3	6	18	33	116	22	3.5		Yes		Yes
Mazokohamena	2010	2	3	6	8	31	0	3.9				Yes
Tsiandrara	2009–2010	3	2	6	17	47	8	3.2	Yes	Yes		
Total		54	70	169	331	1234	98	3.6				

Table 3. *Propithecus coronatus* density data.

Forest	Year	Survey effort (km)	No. obs.	No. ind.	No. groups/km	No. ind/km	ESW (m)	Density (ind /km ²)	Min CI 95%	Max CI 95%
Ambohibary	2009	15.24	51	202	3.3	13.25	14.5	252	100	636
Antsilaiza	2010	26.14	64	216	2.4	8.263	15.9	229	81	646
Ankarahara	2009	51.68	39	139	0.8	2.689	27.9	46	22	99
Antanimalandy	2009	12.71	21	73	1.7	5.742	24.4	79	9	714
Antrema	2010	24.31	57	247	2.3	10.16	14.3	255	99	660
Antsoherikely	2009	52.13	156	681	3.0	13.06	21.4	309	110	867
Antsoherikely	2010	38.32	56	195	1.5	5.088	33.2	75	14	387
Antsoherikely	2009–2010	90.46	212	876	2.3	9.684	25.1	188	93	381
Global analysis		220.54	444	1753	2.1	8.3	20.4	171	115	255

No. obs. = Number of observations; No. ind. = number of sighted individuals; No. groups/km = average number of groups/km; No. ind/km = average number of individuals/km; ESW = effective strip width; CI: confidence interval.

Table 4. Estimated area of occupancy of the crowned sifaka and the total population size.

GIS Data Source	Forest	Year	a: Area (km ²)	b: Min. density (ind/km ²)	c: Average density (ind/km ²)	Minimum population size estimate (ind.) (a × b)	Maximum population size estimate (ind.) (a × c)
Kew	All forests	1999–2000	4148.66	49	171	203285	709422
USAID	All forests	2005	2353.57	49	171	115325	402460
Kew	Mahavavy	1999–2000	208.70	49	171	10226	35688
USAID	Mahavavy	2005	85.28	49	171	4179	14583
Kew	Antrema	1999–2000	5.76	49	171	282	984
USAID	Antrema	2005	0.96	49	171	47	164
Kew	Mahavavy + Antrema	1999–2000	214.46	49	171	10508	36672
USAID	Mahavavy + Antrema	2005	86.24	49	171	4226	14747

Antrema (Table 3). We found lower ESW and higher densities for the census carried out in Antsoherikely in 2009 (ESW = 21.4 and D = 309) than for the censuses made in 2010 (ESW = 33.2, D = 75). This discrepancy was surprising at first but a closer look at the data suggests that the higher ESW values in 2010 result from several observations of groups located on the edges of neighboring fragments (i.e., across open habitat) at distances of 30 to 70 m. When the results obtained for the same transect in 2009 and 2010 were compared, they were actually very similar, suggesting that the high density results are still valid here (data not shown).

The two different GIS datasets showed some discrepancies. We found that the 1999–2000 Kew Garden GIS (Moat and Smith 2007) dataset tended to overestimate forest areas, based on our field observations. This could be due to the fact that data were obtained from 1999 and 2000 Landsat images. On the other hand, the 2005 MEFT-USAID-CI (2009) GIS dataset was found, based on our field observations, to underestimate the size of forests in several cases. Consequently, we used both GIS datasets in order to provide low and high population size estimates.

Using the lowest density estimate (Ankarahara, 46 ind/km²) and applying it to the available habitat calculated using USAID GIS data of 2005 (2,353 km²), indicates a minimum estimate of the total number of *P. coronatus* across the whole forested area of 115,325 individuals (Table 4). If we use the average value of density (171 ind/km²), we obtain 402,460 individuals (Table 4). When performing the estimation with the Kew Garden GIS data of 1999–2000, we obtain population sizes of 203,285 and 709,422 individuals, using the minimum and average densities, respectively. These values should be regarded with caution as there are many uncertainties regarding the calculations, but they probably represent the best available estimates for the global abundance of *P. coronatus*, at the time that the GIS data sets were built. Given that the highest densities may be due to the concentration of *P. coronatus* individuals in the remaining forests, as a consequence of forest loss, a likely figure is possibly closer to our lower estimate; around 100,000 sifakas.

Discussion

Population density and size

The density of *P. coronatus* was shown to vary among fragments, from a low of 46 ind/km² to a high of 309 ind/km². Previous studies published by different authors found values that were even more variable, with values of 5 ind/km² to 500 ind/km² (Curtis *et al.* 1998 and Müller 1997, respectively). How all these values compare is difficult to say since they were produced using different methods. The discrepancies between our density estimates and those of Curtis (1998), who found 5 ind/km² and 32 ind/km² in Katsepy and Anjamena, respectively, could be explained by the different methodologies. Some other previous studies appear to produce more reasonable estimates. For instance, Müller *et al.* (2000) found density values similar to ours in the same area. Moreover, our

results for Antrema (255 ind/km²) are on the same order as those estimated by Pichon *et al.* (2010; >300 ind/km²) also in Antrema. It is worth noting that we combined the Badrara forest (surveyed by Pichon *et al.* 2010) together with a forest located east of Antrema next to the Katsepy lighthouse. When we performed the distance analysis using only the Badrara forest, we also obtained a density estimate of 350 ind/km², thereby confirming consistency between Pichon *et al.* (2010) and our results. The fact that our study was performed in different habitats, some of which were suitable for sifakas (Antsilaiza, Antsoherikely, Antrema-Badrara) and others much less so (i.e., secondary, degraded, or partly cleared forest; Ankarahara, Antsoherikely, Antrema-Katsepy), suggests that our estimates are not major overestimates of population densities for *P. coronatus*.

When we compare our estimates with those published for other sifaka species, we also find that our results fit reasonably well (Table 5). If we exclude the case of *P. perrieri*, one of the most endangered primates of the world with a density of 3.11 ind/km² (Banks *et al.* 2007), the densities published for *P. verreauxi* (Kelley *et al.* 2007) and *P. tattersalli* (Quéméré *et al.* 2010; Table 5) are also of the same order as those obtained here.

Altogether this suggests that estimates of abundance can be reasonably drawn from our density calculations. As we see below, there are, however, many uncertainties, which still require some caution. By extrapolating our results to the likely range of *P. coronatus*, we found that the total abundance probably ranged between 115,325 and 402,425 individuals. Even if we limit ourselves to the six surveyed localities, which represent only a small part of the total geographic range of the species, we find a total of 4,226 to 14,747 individuals with the USAID data and between 10,508 and 36,672 individuals with the Kew Garden data. Moreover, the presence-absence survey showed that there were at least 1,234 independent individuals.

To estimate the area of occupancy of crowned sifakas we took into account all identified forests. This could lead to an overestimation of the total population size since some may not be large enough to host crowned sifaka. The environmental conditions also vary considerably between the northern and southern parts of this broad geographic range. Total size estimates are only based on north-western density estimates and could thus be biased towards lower or higher density in the southern region.

Total population size estimates between 100,000 and 400,000 appear to be very high, but if we compare them to the recent estimates of *P. tattersalli* (>11,000 and probably around 18,000 individuals, Quéméré *et al.* 2010; Table 5), a Critically Endangered sifaka with an area of occupancy less than one tenth that of *P. coronatus*, the new estimates appear more reasonable. Nevertheless, it is important that they should be confirmed by field work carried out in the regions that have until now been little visited. Until then, it might be more reasonable to first consider the estimates which correspond to the region that we have actually studied, i.e., a total abundance between approximately 4,000 and 36,000 individuals.

Most of the remaining geographic range of *P. coronatus* is to a large extent unexplored and lacks even basic data on the presence or absence of populations. Moreover, the areas not explored here are mostly unprotected, with the exception

of the recently established community-based conservation program around the Dabolava-Miandrivazo region. The Bet-siboka-Ikopa region remains to be more carefully surveyed in order to determine if the species was ever or is still present.

Table 5: Sifaka density and population size estimates in the literature.

Species	Site	Density (ind /km ²)	Estimated population size	Analysis method	Field method	Reference
<i>P. coronatus</i>	Anjamena	543		Home range size		Müller (1997)
<i>P. coronatus</i>	Antrema	>300		Complete census		Pichon <i>et al.</i> (2010)
<i>P. coronatus</i>	Anjamena	172.6		LT-DS	Müller	Müller <i>et al.</i> (2000)
<i>P. coronatus</i>	Katsepy	5		Walk and count	Ind./estimated area	Curtis <i>et al.</i> (1998)
<i>P. coronatus</i>	Anjamena	32		Walk and count	Ind./estimated area	Curtis <i>et al.</i> (1998)
<i>P. coronatus</i>	North-west	49 to 309	131,852 to 220,165	LT-DS	CDS	This study
<i>P. deckenii</i>	North-west	3 to 23		Walk and count	Ind./estimated area	Curtis <i>et al.</i> (1998)
<i>P. verreauxi</i>	Kirindy	41 to 1036		Complete census		Norscia and Palagi (2008)
<i>P. coquereli</i>	Ampijoroa	60		Home range size		Richard (1978) in Ganzhorn (1988)
<i>P. tattersalli</i>	Daraina region	34 to 90	11,185 to 26,011	LT-DS	CDS	Quéméré <i>et al.</i> (2010)
<i>P. tattersalli</i>	Daraina region	17 to 28	6,100 to 10,000	LT-DS and Fixed Observation Point		Vargas <i>et al.</i> (2002)
<i>P. edwardsii</i>	Antserananoby	49		LT-DS	CDS	Kelley <i>et al.</i> (2007)
<i>P. edwardsii</i>	Vohibola	2 to 73		LT-DS	Whitesides	Lehmann <i>et al.</i> (2006)
<i>P. edwardsii</i>	South-east	7.65		LT-DS	Whitesides	Irwin <i>et al.</i> (2005)
<i>P. diadema</i>	Tsinjoarivo	7.61 to 20.4		Home range size		Irwin <i>et al.</i> (2008)
<i>P. candidus</i>	Makira	1.5 to 23.1		LT-DS	MPD	Rasolofoson <i>et al.</i> (2007)
<i>P. candidus</i>	Marojejy	40 to 90		LT-DS and random walking	Minimum convex polygon	Sterling <i>et al.</i> (2000)
<i>P. perrieri</i>	Analamenara	3.11	915	LT-DS	Whitesides	Banks <i>et al.</i> (2007)
<i>P. perrieri</i>	North	18 to 21.4	2000	LT-DS and home range size		Meyers and Ratsirarson, (1989)

LT-DS: Line transect-distance sampling; Field method: Müller (Müller *et al.* 2002); CDS: Conventional Distance Sampling (Buckland *et al.* 2001); Whitesides (Whitesides, 1988); MPD: Mean Perpendicular Distance (Gates *et al.* 1968).

Table 6: Conservation status update for crowned sifaka (*Propithecus coronatus*).

IUCN criterion	<i>P. coronatus</i>
Category: Critically Endangered:	
Criterion A – “Reduction in population size” >80%	?
Criterion B – “Geographic range” Area of occurrence <100 km ²	No
Criterion C – “Population size estimated” <250 ind	No
Criterion D – “Populationsize estimated” <50 ind	No
Criterion E – “50% probability of extinction within 10 years”	No
Category Endangered:	
Criterion A – “Reduction in population size” + any of a to e	
1) >70% and ceased, reversible, and understood	No
2) >50% not ceased, not reversible, not understood (10 years/3 generation)	?
3) >50% in the future	?
4) >50% within past and future	Yes, probable
(a) Direct observation	Hunting and deforestation observed
(b) An index of abundance appropriate to the taxon	No
(c) A decline in area of occupancy, extent of occurrence and/or quality of habitat	Probable in last and future 20 years
(d) Actual or potential levels of exploitation	Hunting and deforestation observed
(e) Effects of introduced taxa, hybridization, pathogens, pollutants	?
Criterion B – “Geographic range” Area of occurrence <5000 km ²	No
Criterion C – “Population size estimated” <2500 ind. and other criteria	No
Criterion D – “Population size estimated” <250 ind.	No
Criterion E – “20% probability of extinction within 20 years or five generations”	No
Conclusion	Endangered B1ab

Furthermore, the range of *P. coronatus* remains to be clarified between the Manambolo and Tsiribihina rivers, where only one study has reported its presence (Thalmann and Rakotoarison 1994) but where *P. verreauxi* was also surprisingly reported (ZICOMA 1998, in Wilmé *et al.* 2006).

We should also stress here that most of those areas are located in “dangerous” zones due to the presence of “Dahalo” (Zebu thieves) groups and are furthermore difficult to reach. Given that these regions may harbor the majority of the species’ population, the figures presented here could be over-optimistic if it was found in the future that most crowned sifakas have actually been hunted or burnt along with the forests. A long-term conservation strategy incorporating extended monitoring will require surveys to be carried out in these regions, but safety concerns may make such surveys difficult to implement in the near future.

Implication for conservation

During our survey many blowpipe darts were found in the forests neighboring the Mahavavy River. One of these darts was spotted with blood and had white hair stuck on it, thus strongly suggesting that it was used for hunting sifaka. While local populations do not normally hunt sifakas as they are protected by local taboos (“fady”), some people do not necessarily adopt this taboo and may still hunt them. In Antanimandry, local people repeatedly mentioned the events of the 2008 dry season, when a group of a dozen of hunters came to their village, hired guides and hunted dozens of sifakas every day during one week in the Ankarahara area. This may explain the low densities estimated there in comparison to other neighboring localities (Ambohibary and Antsoherikely). In Mataitromby, sifaka hunting also occurred in 2008 and was apparently and surprisingly carried out by armed forces. Between Ankarabato and Antsalatsala, we found no inhabited villages due to the presence of “Dahalo,” and the remaining forest fragments had been burned or were burning during our visit. More recently, in 2010, the two sifaka groups living next to the Katsepy lighthouse were hunted by “unknown” military men (Peace Corps pers. comm.). Finally, the Tsiamarakely and Tsiamarabe forests in the south of Boeny Aranta had burned a few years before our 2010 visit and were no longer suitable for crowned sifaka and we only found a few individuals. These observations are important in the way that they are testimonies of the threats against crowned sifaka populations and the voluntary or involuntary ignorance of existing regulations.

Finally, using the bibliographical data, our surveys, and the Kew Garden and USAID GIS data we estimated the crowned sifaka area of occupancy to be between 4,493 km² and 2,690 km², respectively, hence confirming that the species should be maintained as Endangered on the basis of the IUCN B1 criterion. We argue, however, that the conservation status of crowned sifakas should be modified from “En A2cd” to “En A4acd” (Table 6). Indeed the current A2cd status is based mainly on assumptions that are difficult to verify (i.e., a reduction of the population size of 50% in the last 10 years

or 3 generations). Given that the deforestation rate across the known area of occupancy of *P. coronatus* was of ~11% between 1990 and 2005 (calculated using CI/USAID deforestation analysis, MEFT, USAID, CI, 2009), and the long generation time recently suggested by Lawler *et al.* (2007) for *P. verreauxi*, this suggests that the population probably decreased by 20–30% in the last 3 generations. Nevertheless the Endangered A4 status is also warranted if a species is suspected to have undergone a reduction of 50% considering both recent past and present rates. Considering that both deforestation (for charcoal production and timber export) and hunting rates have significantly increased after the 2009 political events, it seems reasonable to suspect that crowned sifaka’s populations have unfortunately undergone and will undergo a decline of more than 50% in the ongoing three generations. This proposition (the change from “En A2cd” to “En A4acd”) was recently presented and approved at the 2012 IUCN/SSC Primate Specialist Group Lemur Red-Listing and Conservation-Planning Workshop held in Antananarivo in July 2012.

Conclusion

Our results suggest that there are more *P. coronatus* individuals across the whole geographic range than was previously thought. Although the exact number is difficult to estimate with certainty, it seems reasonable to indicate that it is probably above 10,000 in the northern part of its distribution and possibly around (and larger than) 100,000 across the species’ range. While these figures are higher than originally expected, it is important to note that they represent an extrapolation across the crowned sifaka distribution range on the basis of results obtained in the northern part of its range, using only forest cover and ignoring possible changes in forest cover related to climate change. Finally, using the bibliographical data, survey and GIS data we argue for a change of conservation status criteria for the crowned sifaka from “En A2cd” to “En A4acd”.

Acknowledgments

We thank CAFF/CORE, the ‘Direction Générale des Environnement et Forêts’ and Madagascar National Parks/ANGAP for giving us permission to conduct this study. Financial support was provided by the Fundação para a Ciência e a Tecnologia [FCT, ref. PTDC/BIA-BEC/100176/2008, and SFRH/BD/64875/2009], the Institut Français de la Biodiversité, Programme Biodiversité de l’Océan Indien [ref. CD-AOOI-07-003], the GDRI Madagascar, the «Laboratoire d’Excellence (LABEX)» entitled TULIP (ANR -10-LABX-41), the Instituto Gulbenkian de Ciência, and the “Optimus Alive!” Biodiversity grant. The field work was possible thanks to the continuous support of the University of Mahajanga, the Département de Biologie Animale et Ecologie, the Fanamby NGO [in particular S. Rajaobelina and B.D. Razafindrakoto]. We also acknowledge R. Rabarisoa and C. Nirina from Asity Madagascar, and C.A. Gauthier and V. Vavindrara from the

Antrema SFUM for allowing us to visit their conservation sites. We also thank J. Razafindramanana for actively involving us in this project and M. Irwin, C. Schwitzer, T. King and A. B. Rylands for the constructive reviews on the manuscript and R. Zaranaina and A. Finomana who actively took part in the field work. This study was made in accordance with the laws of the countries of Portugal, France and Madagascar.

Literature Cited

- Baillie, J. and B. Groombridge. 1996. *1996 IUCN Red List of Threatened Animals*. IUCN – The World Conservation Union, Gland, Switzerland.
- Banks, M. A., E. R. Ellis and P. C. Wright. 2007. Global population size of a critically endangered lemur, Perrier's sifaka. *Anim. Conserv.* 10: 254–262.
- Buckland, S. T. 2001. *Introduction to Distance Sampling: Estimating Abundance of Biological Populations*. Oxford University Press, Oxford.
- Curtis, D. J., A. Velo, E. O. Rahelarisoa, A. Zaramody and P. Müller. 1998. Surveys on *Propithecus verreauxi deckeni*, a melanistic variant, and *P. v. coronatus* in north-west Madagascar. *Oryx* 32: 157–164.
- Ganzhorn, J. U. 1988. Food partitioning among Malagasy primates. *Oecologia* 75:436–450.
- Gates, C. E. Marshall, W. H. and Olson, D. P. 1968. Line transect method of estimating grouse population densities. *Biometrics* 24:135–145.
- Irwin, M. T. 2008. Diademed sifaka (*Propithecus diadema*) ranging and habitat use in continuous and fragmented forest: higher density but lower viability in fragments? *Biotropica* 40: 231–240.
- Irwin, M. T., S. E. Johnson and P. C. Wright. 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.
- IUCN. 2008. *2008 IUCN Red List of Threatened Species*. International Union for Conservation of Nature (IUCN), Species Survival Commission, Gland, Switzerland and Cambridge, UK. Website: <<http://www.iucnredlist.org/>>. Accessed 22 October 2011.
- Kaudern, W. 1915. *Säugetiere aus Madagaskar* 9: 1–101.
- Kelley, E. A., R. W. Sussman, K. M. Muldoon. 2007. The status of lemur species at Antserananomby: an update. *Primate Conserv.* (22): 71–77.
- Lawler, R. R. 2007. Fitness and extra-group reproduction in male Verreaux's sifaka: an analysis of reproductive success from 1989–1999. *Am. J. Phys. Anthropol.* 132: 267–277.
- Lehman, S. M., A. Rajaonson and S. Day. 2006. Edge effects and their influence on lemur density and distribution in southeast Madagascar. *Am. J. Physical Anthropol.* 129: 232–241.
- MEFT, USAID, CI. 2009. Rapport final sur l'évolution de la couverture forestière naturelle entre 2000–2005. 58pp. + 66 pp. (annexes) + 22 cartes régionales, Antananarivo, Madagascar.
- Meyers, D. M. and J. Ratsirarson. 1989. Distribution and conservation of two endangered sifakas in northern Madagascar. *Primate Conserv.* (10): 81–86.
- Mittermeier, R. A., E. E. Louis, M. Richardson, C. Schwitzer, O. Langrand, A. B. Rylands, A. F. A. Hawkins, S. Rajabelina, J. Ratsimbazafy, R. Rasoloarison M, C. Roos, P. M. Kappeler and J. Mackinnon. 2010. *Lemurs of Madagascar*. 3rd edition. Conservation International Arlington, VA.
- Moat, J. and P. Smith. 2007. *Atlas of the Vegetation of Madagascar / Atlas de la Végétation de Madagascar*. Royal Botanic Gardens, Kew, London.
- Müller, P. 1997. Ökologie und Ernährungsstrategie des Kronensifakas (*Propithecus verreauxi coronatus*). PhD thesis, Universität Zürich, Zürich.
- Müller, P., A. Velo, E. O. Rahelarisoa, A. Zaramody and D. J. Curtis. 2000. Surveys of sympatric lemurs at Anjamena, north-west Madagascar. *Afr. J. Ecol.* 38: 248–257.
- Norscia, I. and E. Palagi. 2008. Berenty 2006: census of *Propithecus verreauxi* and possible evidence of population stress. *Int. J. Primatol.* 29: 1099–1115.
- Peres, C. A. 1999. General guidelines for standardizing line-transect surveys of tropical forest primates. *Neotrop. Primates* 7: 11–16.
- Petter, J. J. and S. Andriatsarafara. 1987. Conservation status and distribution of lemurs in west and north-west Madagascar. *Primate Conserv.* (8): 169–171.
- Pichon, C., L. Tarnaud, F. Bayart, A. Hladik, C. M. Hladik and B. Simmen. 2010. Feeding ecology of the crowned sifaka (*Propithecus coronatus*) in a coastal dry forest in northwest Madagascar (SFUM, Antrema). *Lemur News* 15: 43–47.
- Plumptre, A. J. and V. Reynolds. 1994. The effect of selective logging on the primate populations in the Budongo Forest Reserve, Uganda. *J. Appl. Ecol.* 31: 631–641.
- Quéméré, E., J. Champeau, A. Besolo, E. Rasolondraibe, C. Rabarivola, B. Crouau-Roy and L. Chikhi. 2010. Spatial variation in density and total size estimates in fragmented primate populations: the golden-crowned sifaka (*Propithecus tattersalli*). *Am. J. Primatol.* 72: 72–80.
- Randrianarisoa, M., A. Ramarison, L. Rakotozafy and A. Totovalahy, 2001. Inventaire des lémuriens dans la Réserve Spéciale de Kasijy. *Lemur News* 6: 7–8.
- Rakotonirina, L. H. F., F. Randriantsara, A. H. Rakotoarisoa, R. Rakotondrabe, J. Razafindramanana, J. Ratsimbazafy and T. King. This issue. A preliminary assessment of sifaka (*Propithecus* spp.) distribution, chromatic variation and conservation in western central Madagascar. *Primate Conserv.* In press.
- Rasolofoson, D., G. Rakotondratsimba, O. Rakotonirainy, T. Rasolofoharivelo, L. Rakotozafy, J. Ratsimbazafy, F. Ratelolahy, V. Andriamaholy and A. Sarovy. 2007. Le bloc forestier de Makira charnière de Lémuriens. *Lemur News* 12: 49–53.

- Rasoloharijaona, S., B. Randrianambinina, B. Rakotosamimanana and E. Zimmermann. 2005. Inventaires des lémuriens dans la forêt d'Andranovelona/Madirovalo (nord ouest de Madagascar), les « savoka » de Manehoko, la Réserve de Lokobe, la Réserve Spéciale de l'Ankarana, et le Réserve Spéciale d'Analamerana, au nord de Madagascar. *Lemur News* 10: 8–11.
- Razafindramanana, J. and R. Rasamimanana. 2010. Discovery of crowned sifaka (*Propithecus coronatus*) in Dabolava, Miandrivazo, Menabe Region. *Lemur News* 15: 23.
- Richard, A. F., R. E. Dewar, M. Schwartz and J. Ratsirarson. 2002. Life in the slow lane? Demography and life histories of male and female sifaka (*Propithecus verreauxi verreauxi*). *J. Zool., Lond.* 256: 421–436.
- Sterling, E. and K. McFadden. 2000. Rapid census of lemur populations in the Parc National de Marojejy, Madagascar. *Fieldiana Zoology* (97): 265–274.
- Sussman, R. W. 1977. Distribution of the Malagasy lemurs part 2: *Lemur catta* and *Lemur fulvus* in southern and western Madagascar. *Ann. New York Acad. Sci.* 293:170–184.
- Tattersall, I. 1986. Notes on the distribution and taxonomic status of some subspecies of *Propithecus* in Madagascar. *Folia Primatol.* 46: 51–63.
- Thalmann, U. and N. Rakotoarison. 1994. Distribution of lemurs in central western Madagascar, with a regional distribution hypothesis. *Folia Primatol.* 63: 156–161.
- Thalmann, U., R. Kümmerli and A. Zaramody. 2002. Why *Propithecus verreauxi deckeni* and *P. v. coronatus* are valid taxa—quantitative and qualitative arguments. *Lemur News* 7: 11–16.
- Thomas, L., S. T. Buckland, E. A. Rexstad, J. L. Laake, S. Strindberg, S. L. Hedley, J. R. B. Bishop, T. A. Marques and K. P. Burnham. 2010. Distance software: design and analysis of distance sampling surveys for estimating population size. *J. Appl. Ecol.* 47: 5–14.
- Vargas, A., I. Jiménez, F. Palomares and M. J. Palacios. 2002. Distribution, status, and conservation needs of the golden-crowned sifaka (*Propithecus tattersalli*). *Biol. Conserv.* 108: 325–334.
- 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.
- Wilmé, L. and M. Callmander. 2006. Les populations reliques de primates: les Propitheques. *Lemur News* 11: 24–31.
- Wilmé, L., S. M. Goodman and J. U. Ganzhorn. 2006. Biogeographic evolution of Madagascar's microendemic biota. *Science* 312: 1063.

Authors' addresses:

Jordi Salmona, Fabien Jan, Sam Viana Meyler, Instituto Gulbenkian de Ciência, Rua da Quinta Grande, 6, P-2780-156 Oeiras, Portugal, **Emmanuel Rasolondraibe, Aubin Besolo, Heriniaina Rakotoarisoa**, Cité Universitaire, Université de Mahajanga, Campus Universitaire Ambondrona, BP 652 401, Mahajanga, Madagascar, **Clément Rabarivola**, Université de Mahajanga, Faculté des Sciences, Campus Universitaire Ambondrona BP 652 401 Mahajanga, Madagascar, **Sébastien Wohlhauser**, Fanamby NGO, Lot II K 39 bis, Ankadivato, 101 Antananarivo, Madagascar, and **Lounès Chikhi**, Population and Conservation Genetics Group, Instituto Gulbenkian de Ciência, Rua da Quinta Grande, 6, P-2780-156 Oeiras, Portugal, CNRS, Université Paul Sabatier, ENFA. UMR 5174 EDB (Laboratoire Evolution & Diversité Biologique), 118 route de Narbonne, F-31062 Toulouse, France, and Université de Toulouse, UMR 5174 EDB, F-31062 Toulouse, France. *Corresponding author*: Jordi Salmona, e-mail: <jordi.salmona@gmail.com>.

Submitted for publication: 2 July 2011

Revised: 31 October 2011