

A Preliminary Assessment of Sifaka (*Propithecus*) Distribution, Chromatic Variation and Conservation in Western Central Madagascar

Authors: Rakotonirina, Laingoniaina Herifito Fidèle, Randriantsara, Fetraharimalala, Rakotoarisoa, Andoniaina Harilala, Rakotondrabe, Rado, Razafindramanana, Josia, et al.

Source: *Primate Conservation*, 2014(28) : 43-53

Published By: Conservation International

URL: <https://doi.org/10.1896/052.028.0116>

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.

A Preliminary Assessment of Sifaka (*Propithecus*) Distribution, Chromatic Variation and Conservation in Western Central Madagascar

Laingoniaina Herifito Fidèle Rakotonirina^{1,2}, Fetraharimalala Randriantsara², Andoniaina Harilala Rakotoarisoa², Rado Rakotondrabe², Josia Razafindramanana^{1,2}, Jonah Ratsimbazafy² and Tony King¹

¹The Aspinall Foundation, Antananarivo, Madagascar

²Groupe d'Etude et de Recherche sur les Primates de Madagascar (GERP), Antananarivo, Madagascar

Abstract: To help inform conservation efforts for the Endangered crowned sifaka *Propithecus coronatus*, in 2010, we attempted to better define the known distribution of sifakas in western central Madagascar through field surveys of 17 sites we considered likely to fall in or close to the historic range of *P. coronatus*. We observed *P. coronatus* at seven sites, in the Boeny, Betsiboka and Bongolava regions. At three sites at the intersection of the regions of Bongolava, Melaky and Menabe we observed populations containing sifaka of *P. deckenii* appearance mixed with melanistic individuals. We observed *P. verreauxi* at the two most southerly sites, in the Amoron'i Mania Region, and *P. coquereli* at one north-easterly site in the Betsiboka Region, a southern extension of 90 km to the known range of the species. At the four remaining sites, sifaka appeared to be either absent or extinct. We observed two other lemur species, *Eulemur mongoz* in the Boeny Region, and *E. rufus* in the Betsiboka Region, the latter observation being a small extension to the species' known range. We noted variation in pelage coloration amongst the *P. coronatus* individuals we observed, mainly regarding the extent and tone of the rufous wash on the back, arms and legs, but also in the color of the head, and the presence or absence of dark patches on the nape or at the root of the tail. The melanistic forms of *P. deckenii* varied greatly, some being very dark brown on large areas of the head, back, arms and legs, and appearing unlike any typical sifaka species, others exhibiting an intermediate coloration fairly similar to *P. coronatus*. We therefore suggest that *P. coronatus* should not be considered to represent an extreme melanistic form of *P. deckenii*, and that most previous reports of possible sympatry between the two taxa might alternatively be explained by a melanistic tendency in *P. deckenii*, possibly arising from occasional gene flow from *P. coronatus*. Our results show that *P. coronatus* may now be considered widely distributed through western central Madagascar, but most forests in this area are small and fragmented, and sifaka populations are highly endangered. We therefore recommend the implementation of immediate conservation interventions to ensure the maintenance of the full range of chromatic and genetic diversity of *P. coronatus*.

Key Words: *Propithecus coronatus*, *Propithecus deckenii*, *Propithecus coquereli*, *Eulemur rufus*, *Eulemur mongoz*, gene flow, melanism

Introduction

The crowned sifaka *Propithecus coronatus* is classified on the IUCN Red List as Endangered (IUCN 2012). It appears to have a poorly-known range in the wild, with the largest known populations surviving in the fragmented, dry deciduous forests between the Betsiboka and Mahavavy rivers in north-west Madagascar (Mittermeier *et al.* 2010; Salmona *et al.* this issue). To the north and east of the Betsiboka River it is replaced by Coquerel's sifaka *P. coquereli*, and to the south and west of the Mahavavy river by Decken's sifaka *P. deckenii* (Mittermeier *et al.* 2010). Populations of *P. coronatus* have

also been reported in fragmented forests in the Boeny and Bongolava regions south to Tsiroanomandidy and the Sakay River (Milne-Edwards and Grandidier 1875; Tattersall 1986; Thalmann *et al.* 2002; Mittermeier *et al.* 2010), and the most southerly known site was recently discovered in the Menabe Region near Miandrivazo (Razafindramanana and Rasamimanana 2010). To the south and south-west of its range the species is replaced by Verreaux's sifaka *P. verreauxi* (Mittermeier *et al.* 2010; Razafindramanana and Rasamimanana 2010).

This general distribution of these four sifaka species is, however, not quite as neat as we have just described. Several taxonomic and distributional issues regarding this group remain

unresolved. Historically, many authors considered them all as subspecies of *P. verreauxi* (Hill 1935; Petter *et al.* 1977; Tattersall 1982), whilst others have proposed that *P. coronatus* and *P. deckenii* are a single taxon, either as a monospecific *P. deckenii*, or as a single subspecies of *P. verreauxi* (Tattersall 1988; Pastorini *et al.* 2001). Several authors have given detailed syntheses elsewhere (Thalmann *et al.* 2002; Groves and Helgen 2007; Mittermeier *et al.* 2008, 2010), so to summarize, much of this discussion concerning *P. coronatus* and *P. deckenii* arises from the observation that sifaka populations in the northern reaches of the Mahavavy River are generally either of *P. coronatus* coloration to the east (white body with a predominantly black head) or of *P. deckenii* coloration to the west (white body with a white head), whilst several observations further south include individuals resembling both forms (Curtis *et al.* 1998; Randrianarisoa *et al.* 2001b; Thalmann *et al.* 2002), or melanistic forms which resemble neither species (Petter and Peyrieras 1972; Petter *et al.* 1977). Further confusion appears to have arisen from equivocal interpretations of written descriptions of pelage variation given in older publications that generally lack photographs or illustrations, and also to some extent the lack of precise coordinates for some observations.

These unresolved issues have several consequences for conservation, not least because the conservation status of a taxon depends on which populations are included within it, and also because in developing a conservation program,

planners need to define what they are attempting to conserve (Blair *et al.* 2011). They also need to be confident that they know the distribution of a taxon, in order to be able to assess its abundance and status, and to design appropriate conservation interventions (Rakotonirina *et al.* 2011). Within the framework of a conservation project for *P. coronatus* (The Aspinall Foundation 2009, 2010), we therefore attempted to better define the known distribution of the species through field surveys of sites in western central Madagascar that we considered likely to fall within or close to its historic range. In this paper we present the results of our survey work during 2010, including newly-reported sites supporting sifakas, descriptions and photographs of the pelage variation we found within sifaka populations at these sites, and preliminary assessments of the threats they face at each.

Methods

We surveyed 17 sites in 16 communes of six administrative regions of western central Madagascar (Table 1). The six most northerly sites were at low altitude (12 to 384 m) in the Boeny and Betsiboka regions; the remaining 11 sites were at mid to high altitude (657 to 1339 m) in the Bongolava, Melaky, Menabe and Amoron'i Mania regions. We undertook several missions between January and December 2010 to survey all these sites (Table 1). We consulted local authorities

Table 1. Sites surveyed during 2010. Summary of the main results regarding the presence of sifaka and other lemurs.

Region	Commune	Site	Notes	Survey Month	Coordinates	Altitude (m)	Observers ^a
Sites with <i>P. coronatus</i>							
Boeny	Ambato Boeny	Anaboazo	4 groups; also 2 groups of <i>Eulemur mongoz</i>	Nov	16.583°S 46.605°E	12-29	LR, AR
Betsiboka	Mangabe	Maevatanana-Ambato-Boeni Wetlands	5 groups	Nov	16.767°S 46.739°E	22-34	LR, AR
Betsiboka	Madiromirafy	Mandrava	2 groups	Nov	16.847°S 46.782°E	36-46	LR, AR
Betsiboka	Mahazoma	Ikay	1 group; also <i>Eulemur rufus</i>	Oct	17.024°S 46.613°E	53-60	LR, AR
Bongolava	Ambohitromby	Ambohitromby	2 groups	Oct	17.899°S 46.302°E	797-814	LR, AR
Bongolava	Mahajeby	Mahajeby	2 groups	Mar	18.029°S 45.955°E	657-679	LR, FR
Bongolava	Bemahatazana	Andasilaikatsaka	2 groups	Mar	19.306°S 45.876°E	824-1079	LR, FR
Sites with <i>P. deckeni</i> and melanistic forms							
Melaky	Beravina	Fiadanana	5 groups	Aug	18.210°S 45.560°E	1106-1143	LR, FR
Melaky	Beravina	Antsakasarotra	4 groups	Aug	18.257°S 45.427°E	962-1117	LR, FR
Menabe	Soaloka	Orimbato	6 groups in Mar, 7 in Aug	Mar, Aug	18.298°S 45.531°E	1180-1252	LR, FR
Sites with other species, or no sifaka were found							
Betsiboka	Ambalananakomby	Betonendry / Maroakanga	<i>P. coquereli</i>	Oct	17.102°S 47.078°E	331-384	LR, AR
Betsiboka	Antsiafabositra	Bekirobo (Kamoro)	Sifaka apparently extinct ^b	Oct	17.136°S 47.017°E	305	LR, AR
Bongolava	Ambatomainty	Ampandrambe	Sifaka apparently absent	Oct	18.318°S 46.332°E	1092	LR, AR
Menabe	Itondy	Mavoravina Mahazoarivo	Sifaka apparently extinct ^b	Aug	19.076°S 45.553°E	804-1025	LR, FR
Menabe	Manandaza	Tsatananana	Sifaka apparently absent	Aug	19.281°S 45.718°E	800-989	LR, FR
Amoron'i Mania	Mangataboahangy	Andakata - Ambolokely	<i>P. verreauxi</i>	Dec	20.339°S 46.237°E	852-855	RR, AR
Amoron'i Mania	Amborompotsy	Andondona: Analakinganala	<i>P. verreauxi</i>	Jan	20.534°S 46.347°E	1338-1339	RR, AR

^a Observers: LR: Laingoniaina Rakotonirina; FR: Fetraharihalala Randriantsara; AR: Andoniaina Rakotoarisoa; RR: Rado Rakotondrabe.

^b We did not find evidence for sifaka at these sites, but local people claimed that sifaka (of unspecified species) existed there previously.

and local populations in each zone before selecting the precise localities for our surveys at each site. Accompanied by local guides and at some sites by local gendarmes, we searched for sifaka following paths in the forest or by walking along the edge of forest patches or gallery forests. On each occasion that we observed sifaka, we took a GPS point and noted the date and time of the observation, the size of the group, the sex and age-class of each individual wherever possible, and described their coloration. We also noted the presence of any other lemur species we encountered, and any evidence of threats to the sites. Lemur nomenclature follows Mittermeier *et al.* (2010), and vegetation classifications follow Moat and Smith (2007).

Boeny Region

The largest known populations of *P. coronatus* occur in the Boeny Region, particularly in the communes of Katsepy, Antongomena Bevary and Mitsinjo, and have been the focus of several studies (Curtis *et al.* 1998; Muller *et al.* 2000; Pichon *et al.* 2010; Salmona *et al.* this issue). This region was therefore not a priority area for our surveys. However, we did survey one site in the region, Anaboazo in the commune of Ambato Boeny, as we received reliable information regarding the presence of the species in this unprotected and previously unsurveyed forest (M. Mbaraka pers. comm.). The region is the most forested of those we surveyed, consisting of fragmented western dry forest and wooded grassland—bushland and plateau grassland-wooded grassland mosaics (Moat and Smith 2007).

Betsiboka Region

We surveyed five sites in the Betsiboka Region, which apparently had never been reported as supporting *P. coronatus* populations; the Kasijy Special Reserve is located in this region, but supports primarily *P. deckenii*, with only a few individuals that reportedly resemble *P. coronatus* (Randrianarisoa *et al.* 2001b). We selected two of these sites because they were in or near proposed new protected areas (Kamoro and Maevatanana-Ambato-Boeni Wetlands), and the other three due to the apparently large tracts of remaining forest (relative to surrounding areas) and their apparent relative ease of access (based on proximity to roads and other routes). The vegetation present in this region is similar to that of the Boeny Region, but with considerably less forest cover (Moat and Smith 2007).

Bongolava, Menabe and Melaky Regions

The Bongolava Region has long been known to harbor *P. coronatus* populations (Milne-Edwards and Grandidier 1875; Petter and Peyrieras 1972; Petter *et al.* 1977; Tattersall 1986; Petter and Andriatsarafana 1987) but reports are based on only a few observations, some of which lack precise locality data while others provide confusing accounts of variable pelage coloration. This region, along with adjacent areas of the Menabe and Melaky regions that had previously been found to support populations of sifaka containing individuals

resembling both *P. deckenii* and *P. coronatus* and melanistic forms (Petter and Peyrieras 1972; Petter *et al.* 1977; Randrianarisoa *et al.* 2001a; Thalmann *et al.* 2002), was therefore the main focus of our surveys. We visited nine sites across these regions. We chose three of them because they had been proposed as protected areas (Ambohitromby, Mahajeby and Andasilaikatsaka), one due to local information regarding the presence of black-headed white lemurs (Ampandrambe), and the remaining five following the advice of the regional environment and forestry authority (DREF Tsiroanomandidy pers. comm.). This area comprises predominantly wooded grassland—bushland and plateau grassland-wooded grassland mosaics, with only very restricted areas of western dry forest, often as gallery forest along watercourses (Moat and Smith 2007). A relatively large patch of azonal humid forest occurs in and around the Ambohijanahary Special Reserve near the intersection of the three regions (Moat and Smith 2007).

Amoron'i Mania Region

We visited two sites in the Amoron'i Mania Region, in the vicinity of the Itremo new protected area, to verify previous reports that sifaka here were *P. verreauxi* (Wilmé and Callander 2006; Wilmé *et al.* 2006), and therefore confirm the southern limit of *P. coronatus*. The predominant vegetation is classified as a mosaic of plateau grassland and wooded grassland, with gallery forests so limited that they do not show up on the vegetation map of Moat and Smith (2007).

Results

We made direct observations of sifaka at 13 of the 17 survey sites (Table 1; Fig. 1). We observed sifaka appearing to be *P. coronatus* at seven sites, in the Boeny, Betsiboka and Bongolava regions (Tables 1 and 2; Fig. 2). At three sites in the Melaky and Menabe regions we observed populations of sifaka of *P. deckenii* appearance mixed with melanistic individuals (Tables 1 and 2; Fig. 3). We found *P. verreauxi* at the two most southerly sites, in the Amoron'i Mania Region, and *P. coquereli* at one north-easterly site in the Betsiboka Region (Table 1; Fig. 4). At the four remaining sites sifaka appeared to be either absent or extinct (Table 1). We recorded only two other lemurs during the surveys; *Eulemur mongoz* at Anaboazo and *Eulemur rufus* at Ikay (Table 1; Fig. 4).

We noted variation in pelage coloration amongst the *P. coronatus* individuals we observed, mainly regarding the extent and tone of the rufous wash on the back, arms and legs, but also in the color of the head, and the presence or absence of dark patches on the nape or at the root of the tail (Table 3; Fig. 2). The most heavily-colored individuals occurred at the Andasilaikatsaka site, whilst at the other sites the within-site variation between individuals appeared to be similar to the between-site variation (Table 3; Fig. 2).

At the three sites where we recorded *P. deckenii*, 80% of individuals we observed (60 of 80) were of typical *P. deckenii* coloration (predominantly white with a black face), with a few that were lightly-washed golden on the back, and very rarely

with a darkish patch on the nape (Table 4; Fig. 3). The remaining 20% exhibited varying degrees of melanism, which for the sake of simplicity we split into two forms for the pelage descriptions, the “intermediate” form of which some could be described as being similar to *P. coronatus* in coloration, and the “very dark” form which is very dark brown on large areas of the head, back, arms and legs, and is unlike any typical sifaka species (Table 4; Fig. 3). Of 22 sifaka groups observed at these three sites, 13 (59%) consisted of only white individuals, one (5%) of only melanistic individuals, and eight (36%) of both white and melanistic forms (Table 2). During

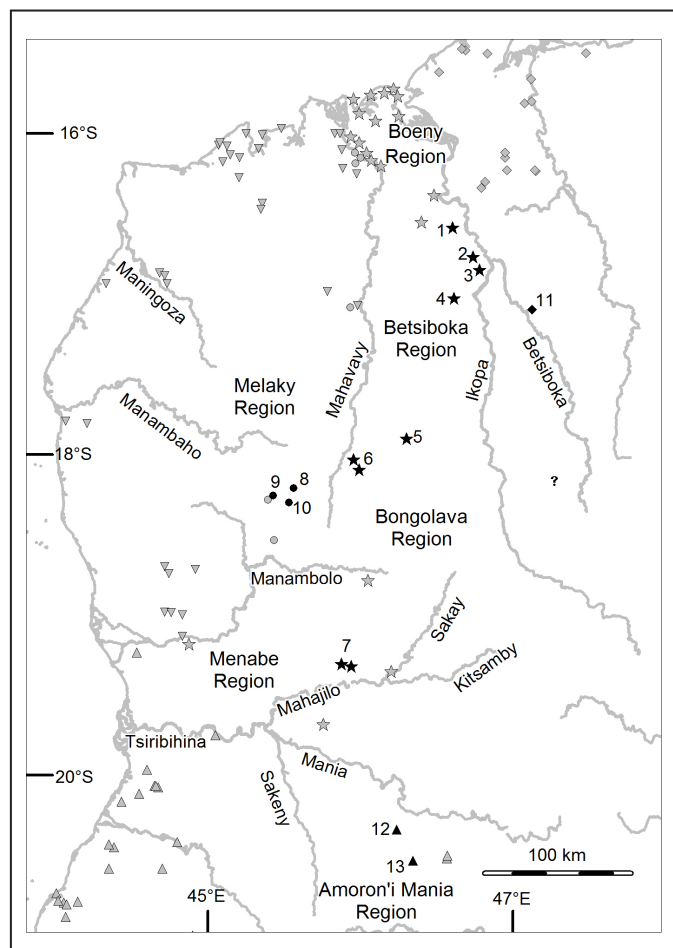


Figure 1. Map of west and western central Madagascar showing distributional records of four sifaka species in relation to regions and major rivers. New sites reported here are given as numbered black symbols, and previously published sites as grey symbols, of *P. coronatus* (stars), *P. deckenii* (inverted triangles), *P. deckenii* occurring sympatrically with melanistic forms (circles), Verreaux's sifaka *P. verreauxi* (triangles) and Coquerel's sifaka *P. coquereli* (diamonds). The question mark represents the site of Ambohitantely, where *P. coronatus* is claimed to have occurred in the past by some authors, but the accuracy of this account is questionable. Note that at the site on the south bank of the Manambolo River, one *P. deckenii* was also recorded in addition to six *P. coronatus* (Thalmann and Rakotoarison 1994). Previously published sites are taken principally from Wilmé *et al.* 2006 and references therein, plus additional records from Tattersall (1986), Thalmann and Rakotoarison (1994), Razafindramanana and Rasamimanana (2010), and Salmona *et al.* (this issue); for further details see The Aspinall Foundation (2010). The names of our numbered survey sites are: 1: Anaboazo; 2: Maevatanana-Ambato-Boeni Wetlands; 3: Mandrava; 4: Ikay; 5: Ambohitromby; 6: Mahajeby; 7: Andasilaikatsaka; 8: Fiadanana; 9: Antsakasarotra; 10: Orimbato; 11: Betonendry/Maroakanga; 12: Andakata – Ambolokely; 13: Andondona: Analakinganala.

the August sample period, we twice observed melanistic females carrying white infants, in addition to four instances of white infants carried by white females (Table 2).

The size of the *P. coronatus* groups we observed ranged from one to eight individuals (Table 2; mean = 4.2, sd = 1.83, n = 18), and of groups at the three sites with *P. deckenii* and melanistic forms counts were from one to six individuals (Table 2; mean = 3.4, sd = 1.22, n = 22).

We noted the presence of a number of threats to the sifaka and their habitat at each site (Table 5). Of the ten sites where we observed either *P. coronatus* or *P. deckenii*, we found evidence of hunting of the sifaka at seven sites, and varying degrees of habitat destruction or disturbance at every site (Table 5). The extent of forest cover varied between sites, but at each of the seven sites where we observed *P. coronatus* the forest was fragmented, with a general north to south tendency of decreasing size of fragments and increasing distance between fragments.

Discussion

Distribution of and chromatic variation in P. coronatus and P. deckenii

We report here the first published observations of *P. coronatus* at seven sites in the Boeny, Betsiboka and Bongolava regions, which help refine our understanding of the current range of the species. Comparing our new records with previously published records of *P. coronatus*, *P. deckenii*, *P. verreauxi* and *P. coquereli* (Fig. 1), it appears that *P. coronatus* remains distributed more-or-less throughout the remaining forests of north-west and western central Madagascar, from Katespy in the north to Dabolava in the south, approximately between the Mahavavy River to the west and the Ikopa and/or Betsiboka rivers to the east. There is some uncertainty about whether *P. coronatus* occurs, or has occurred, between the Ikopa and Betsiboka rivers. We failed to find sifaka at the one site we surveyed between these rivers, and the only published record from the area is one of the species having apparently gone extinct at Ambohitantely Special Reserve (Petter and Andriatsarafana 1987). Apparently this record arose, however, from an error in translation (S. Goodman, pers. comm.) and therefore we consider the presence of *P. coronatus* east of the Ikopa River to be unconfirmed. There appears to be even greater confusion about sifaka species limits in the south-west of the *P. coronatus* range (Fig. 1), so we recommend further surveys between the Mahajilo, Manambolo and Tsiribihina rivers to clarify sifaka distributions in this region.

Our reports of three sites in the Melaky and Menabe regions containing sifaka populations comprising individuals of classic *P. deckenii* coloration mixed with individuals exhibiting varying degrees of melanism reflect previously published observations in the Ambohijanahary forest and Special Reserve located 1 to 40 km south of our observations (Randrianarisoa *et al.* 2001a; Thalmann *et al.* 2002), the Kasijy Special Reserve located 140 km north of our sites (Randrianarisoa *et al.* 2001b), and in the Bongolava Massif

(Petter and Peyrieras 1972, reprinted in French by Petter *et al.* 1977), which includes the general region of our observations. These authors all report sifaka populations consisting mostly of white *P. deckenii* individuals, but with varying proportions

of individuals showing melanistic features, and/or individuals closely resembling *P. coronatus*. Unfortunately most of these publications lack photographs or illustrations, and there is a lack of consistency between written descriptions of the

Table 2. Details of groups of *P. coronatus* and *P. deckenii* observed during our survey.

Site	Locality ^a	Date	Latitude	Longitude	Altitude (m)	Group size	Infants	Melanistic
Sites with <i>P. coronatus</i>								
Anaboazo		06/11/2010	16.584°S	46.605°E	27	5	1	0
Anaboazo		06/11/2010	16.585°S	46.607°E	21	4	0	0
Anaboazo		06/11/2010	16.584°S	46.610°E	29	6	1	0
Anaboazo		06/11/2010	16.580°S	46.609°E	19	5	1	0
Maevatanana-Ambato-Boeni Wetlands	Belafika	04/11/2010	16.767°S	46.739°E	22	4	0	0
Maevatanana-Ambato-Boeni Wetlands	Belafika	04/11/2010	16.769°S	46.734°E	21	1	0	0
Maevatanana-Ambato-Boeni Wetlands	Liolava	04/11/2010	16.750°S	46.707°E	26	4	1	0
Maevatanana-Ambato-Boeni Wetlands	Liolava	04/11/2010	16.751°S	46.707°E	23	5	0	0
Maevatanana-Ambato-Boeni Wetlands	Liolava	04/11/2010	16.751°S	46.708°E	21	3	0	0
Mandrava		02/11/2010	16.847°S	46.781°E	36	8	1	0
Mandrava		02/11/2010	16.848°S	46.780°E	46	8	1	0
Ikay		30/10/2010	17.024°S	46.609°E	60	4	1	0
Ambohitromby	Bemoramena	14/10/2010	17.899°S	46.301°E	808	4	1	0
Ambohitromby	Bevoay	14/10/2010	17.899°S	46.304°E	796	2	0	0
Mahajebly	Andafy atsinanan'ny Tongopapango 2	05/03/2010	18.095°S	45.993°E	679	4	0	0
Mahajebly	Betsidriky	06/03/2010	18.029°S	45.955°E	657	2	0	0
Andasilaikatsaka	Andasibemialy	20/03/2010	19.306°S	45.876°E	1079	4	0	0
Andasilaikatsaka	Andranoboky	22/03/2010	19.318°S	45.939°E	824	3	0	0
Sites with <i>P. deckenii</i> and melanistic forms								
Orimbato	Ambalahita	11/03/2010	18.298°S	45.531°E	1180	4	0	2
Orimbato	Ampitandambo	12/03/2010	18.312°S	45.551°E	1227	2	0	0
Orimbato	Ampitandambo	12/03/2010	18.313°S	45.548°E	1221	5	0	3
Orimbato	Ampitandambo	12/03/2010	18.313°S	45.546°E	1211	2	0	0
Orimbato	Antendangisa	13/03/2010	18.312°S	45.571°E	1252	2	0	2
Orimbato	Antendangisa	13/03/2010	18.323°S	45.572°E	1207	4	0	1
Fiadanana	Andoharano	25/08/2010	18.234°S	45.542°E	1126	4	1 ^b	0
Fiadanana	Andoharano	25/08/2010	18.210°S	45.560°E	1124	3	1 ^c	1
Fiadanana	Andoharano	25/08/2010	18.219°S	45.555°E	1143	4	0	3
Fiadanana	Andoharano	25/08/2010	18.224°S	45.545°E	1116	1	0	0
Fiadanana	Andoharano	26/08/2010	18.224°S	45.543°E	1106	3	1 ^b	0
Orimbato	Ankazomajinidravina	26/08/2010	18.259°S	45.555°E	1231	4	1 ^c	1
Orimbato	Ankazondrano	27/08/2010	18.290°S	45.529°E	1207	4	0	0
Orimbato	Ankazondrano	27/08/2010	18.287°S	45.532°E	1192	4	0	0
Orimbato	Ankazondrano	27/08/2010	18.285°S	45.523°E	1202	4	0	0
Orimbato		27/08/2010	18.286°S	45.520°E	1191	6	1 ^b	1
Orimbato	Belalimanga	27/08/2010	18.286°S	45.490°E	1128	4	0	0
Antsakasarotra	Antamponantsakasarotra	27/08/2010	18.257°S	45.427°E	1117	3	0	1
Antsakasarotra		27/08/2010	18.259°S	45.378°E	1014	5	1 ^b	0
Antsakasarotra		27/08/2010	18.258°S	45.379°E	1025	2	0	0
Antsakasarotra		27/08/2010	18.269°S	45.462°E	962	3	0	0
Orimbato		27/08/2010	18.323°S	45.573°E	1175	2	0	0

^a We use the term "locality" to describe specific forest fragments or other locally-named locations within our main survey sites

^b White infant with white adult

^c White infant with melanistic adult



Figure 2. Chromatic variation of *P. coronatus* at the survey sites from the Boeny and Betsiboka regions (top line) and the Bongolava Region (bottom line): Anaboazo (a), Ikay (b and e), Mandrava (c and d), Ambohitromby (f), Mahajeby (g) and Andasilaikatsaka (h-j). Photographs by L. Rakotonirina.

Table 3. Chromatic description of *P. coronatus* observed at the survey sites.

Site	Head	Nape	Back	Outer surface of arms	Outer surface of legs	Chest and abdomen	Root of tail
Anaboazo (Ambato Boeny Region)	Black, dark brown or with reddish tinge	Whitish	Whitish, or lightly rufous on the upper half or through to the base of the tail	Whitish or light to dark rufous	Whitish, some with greyish rufous on thigh	Dark brown / rufous	Whitish or light rufous
Betsiboka Region (three sites)	Black, dark brown, or brownish red	Whitish	Whitish, or lightly rufous on the upper half	Whitish or light to dark rufous	Whitish or very mildly rufous on thigh	Dark brown / rufous	Whitish, or light or dark rufous
Ambohitromby (Bongolava Region)	Black, dark brown or with reddish tinge	Whitish	Whitish, or lightly to heavily washed rufous, especially on the upper half	Whitish or light to dark rufous	Whitish	Dark brown / rufous	Whitish or light rufous
Mahajeby (Bongolava Region)	Black, dark brown or with reddish tinge	Whitish, some with large blackish patch	Whitish, or lightly to heavily washed rufous, especially on the upper half	Whitish, or lightly washed rufous	Whitish	Dark brown / rufous	Light rufous
Andasilaikatsaka (Bongolava Region)	Black, dark brown or with reddish tinge	Whitish, some with small blackish patch	Heavily washed rufous on the upper half	Light or dark rufous, sometimes merging to grey	Whitish, some with rufous on thigh	Dark brown / rufous	Whitish



Figure 3. Chromatic variation of sifaka at the Orimbato site, including typical white *P. deckenii* (a and b), forms that we refer to as intermediate melanistic forms of which some resemble *P. coronatus* (b–e), and very dark melanistic forms which resemble neither *P. deckenii* nor *P. coronatus* (bottom line). Photographs by L. Rakotonirina.

Table 4. Chromatic description of *P. deckenii* and melanistic forms observed at the sites of Fiadanana, Antsakasarotra and Orimbato.

Form	Head	Nape	Back	Outer surface of arms	Outer surface of legs	Chest and abdomen	Tail	Root of tail
White (<i>P. deckenii</i>)	White with a black face (all forms have short white fur across nose to greater or lesser extent)	White, or rarely with blackish patch	White, or mildly tinted gold	White, some very mildly tinted gold	White	Whitish or dark brown	White	White
Melanistic 1 (intermediate)	Black face, surrounded by dark brown mask, light brown to greyish cap, black ears with white tufts, some with whitish fur around cheeks	Light rufous	Light to dark rufous on upper half, light grey lower half	Upper arm dark rufous, fore-arm dark brown on anterior and whitish on posterior aspects	Light grey to whitish on anterior aspect of thigh, whitish elsewhere	Dark brown	Whitish to greyish with faint grey rings	Light rufous
Melanistic 2 (very dark)	Very dark brown or blackish, with small whitish patch on forehead	Light grey or brown, or dark brown	Dark chocolate brown or dark brown in upper half, brownish grey or grey in bottom half	Dark brown on anterior aspect, whitish on posterior aspect	Dark grey or brown on anterior aspect of thigh, whitish elsewhere	Dark brown to black	Whitish to greyish with faint grey rings	Whitish to greyish



Figure 4. *P. verreauxi* at Analakinganala, *P. coquereli* at Betonendry/Maroakanga, *Eulemur rufus* at Ikay, and *E. mongoz* at Anaboazo. Photographs by L. Rakotonirina except those of *P. verreauxi* by R. Rakotondrabe.

Table 5. Threats observed at each of the survey sites where we observed either *P. coronatus* or *P. deckenii*.

	Anaboazo	Mangabe	Mandrava	Ikay	Ambohitromby	Mahajeby	Andasilaikatsaka	Fiadanana	Antsakat-sarotra	Oribato
Hunting	+		+	+	+	+		+	?	+
Logging	+				+			+	+	+
Tree cutting for local use	+	+	+	+	+	+	+	+	+	+
Charcoal production	+	+	+	+	+					+
Forest fires	+	+			+					
Encroachment of bush fires	+	+	+	+	+			+	+	+
Disturbance by domestic cattle	+				+	+	+	+	?	+
Official zonation status	Formerly exploited	Locally managed	?	Pro-tection	Protection	Protection	Protection	Exploitation	?	Protection

variation in pelage coloration. Nevertheless, several of the descriptions (for example, Randrianarisoa *et al.* 2001b at Kasijy, and some of those given by Petter and Peyrieras 1972) can be considered consistent with one or other of the two melanistic forms we describe, the “very dark” and “intermediate” forms, of which the latter resembles *P. coronatus* to a greater or lesser extent depending on the individual. Other descriptions suggest even lighter forms (for example, Randrianarisoa *et al.* 2001a at Ambohijanahary, and one of those given by Petter and Peyrieras 1972), with a whitish or lightly colored head and darker or blackish patches restricted to the nape, upper back and arms. We did not recognize a “light” melanistic form during our surveys, although some of the individuals we considered as white *P. deckenii* did show a dark grey patch on the nape (Table 4). In another area with several reports of sites containing both white *P. deckenii* and darker-colored sifaka, between the Mahavavy River and the Kinkony Lake in

the Boeny Region (Thalmann *et al.* 2002) 250 km north of our *P. deckenii* observations, Curtis *et al.* (1998) describe individuals which appear to resemble our “intermediate” form, but also a “lighter melanistic variant,” which closely resembles a white *P. deckenii* but with a dark brown ventral surface and an off-white to silvery-grey head. Tattersall (1986) describes four museum specimens from approximately the same area with variably pale silver-brown heads (excluding the ears), and pale silver-brown on the anterior aspects of the limbs and the upper back, fading towards the rump; a description that appears to fall between our “intermediate” form and the “light” forms described from elsewhere.

It appears therefore that melanistic forms of *P. deckenii* vary in a fairly continuous manner from “light” forms closely resembling classic white *P. deckenii* with only limited melanistic features, through “intermediate” forms that in some cases resemble *P. coronatus*, to “very dark” forms

that resemble neither *P. coronatus* nor classic *P. deckenii*. We note that dark melanistic adults have been reported with both dark (Petter and Peyrieras 1972) and white infants (Table 2; also Petter and Peyrieras 1972), but that white adults have so far been reported only with white infants (Table 2; also Petter and Peyrieras 1972). Further observations are therefore required to determine whether white females do occasionally produce dark infants or not.

The fact that all reported observations of melanistic individuals of *P. deckenii* are from sites along the eastern boundary of the species range, east of which the species is replaced by *P. coronatus*, suggests that the underlying reason behind this melanistic tendency might be occasional gene flow with *P. coronatus*, with locally plausible scenarios suggested for several of the areas with melanistic *P. deckenii* given by Thalmann *et al.* (2002). If this is the case, however, it is hard to see why this would result in some “very dark” forms much darker than typical members of either species, as we report here, especially as the only reported description of a *deckenii* × *coronatus* hybrid (Petter 1969) appears to resemble our “intermediate” form, or why the majority of individuals in these populations do not show signs of hybridization (Petter and Peyrieras 1972; Petter *et al.* 1977). Given the doubt over the plausibility of the hybridization hypothesis for explaining the melanistic tendencies in *P. deckenii* and some other *Propithecus* species, an alternative hypothesis was given by Petter and Peyrieras (1972) and Petter *et al.* (1977) regarding genetic selection processes related to altitude and climatic factors, with areas of high melanistic tendencies being climatically intermediate between the principle distributional areas of typical forms, and therefore minimizing the impacts of such selection leading to increased expression of variation. Over 35 years on from this discussion the question appears to remain unresolved, and we therefore recommend further research into the subject, incorporating genetic analysis. This would best include all known cases of chromatically-variable sifaka populations, including the interesting population in the eastern rainforest at Tsinjoarivo, which apparently exhibits a range of colorations from all-white to all-black via various forms resembling to a greater or lesser extent the diademed sifaka *P. diadema* (Mittermeier *et al.* 2010, pp.532–533). Such a study could also include the indri *Indri indri*, another member of the Indriidae family which exhibits variable coloration from predominantly black to variegated black-and-white, sometimes within the same populations (Thalmann *et al.* 1993; Zaonarivelo *et al.* 2007; Mittermeier *et al.* 2010).

Despite not understanding the underlying causes, our interpretation of melanistic tendencies in *P. deckenii* implies that the majority of cases of proposed sympatry between *P. deckenii* and *P. coronatus* given in previous literature may alternatively be explained by melanism in *P. deckenii*, and therefore that the two taxa may not actually be sympatric. The occasional observation of *P. deckenii* individuals amongst otherwise *P. coronatus* populations (Tattersall 1982, 1988; Thalmann and Rakotoarison 1994) can probably be explained by local and rare events of *P. deckenii* crossing rivers or other

biogeographical boundaries by one means or another (including possibly escapes or releases of sifaka kept as pets by local people on the opposing bank of a river to where they were captured). The idea that *P. coronatus* might simply represent the extreme end of melanistic tendencies in *P. deckenii* is also not supported by our observations, as “very dark” melanistic *P. deckenii* are considerably darker than *P. coronatus*, and chromatic variation in most known *P. coronatus* populations is relatively limited. There is apparently a slight tendency of increasing rufous coloration on the back and limbs of *P. coronatus*, from the generally whitish forms in the north of the range (Milne-Edwards and Grandidier 1875; Petter and Peyrieras 1972), through the variably whitish to lightly or more heavily washed rufous forms in the southern Boeny Region, the Betsiboka Region, and the northern Bongolava Region (Table 3), to the often (but not always) more heavily washed rufous forms at Andasilaikatsaka in the southern Bongolava Region (Table 3). The only other potential melanistic tendencies that we have observed include the occurrence of a blackish patch on the nape, or a light or dark rufous patch at the root of the tail (Table 3; Fig. 2). We observed the former feature at our two most southerly survey sites, in the Bongolava Region, but the darkest examples of the latter feature were in the Betsiboka Region, approximately in the central region of the species latitudinal range. Some sifaka in the Betsiboka Region also showed the lightest-colored heads of all the survey sites, being a fairly bright brownish red color, whereas elsewhere heads were blackish or dark brown with only a tinge of red (Table 3; Fig. 2).

There appear to be only two prior reports of more extensive melanistic tendencies in *P. coronatus*. One is at the most southerly-known site at Dabolava in the Menabe Region, where some individuals show varying degrees of dark blackish patches on their shoulders, mid-back, and the upper aspects of their arms and thighs (Razafindramanana and Rasamimanana 2010; J. Razafindramanana, unpubl. photos), in a similar pattern to that shown by melanistic variants of *P. verreauxi* (Mittermeier *et al.* 2010, pp. 526–527). The other is the description of a pair of sifakas captured on the track from Tsiroanomandidy to Ankavandra (Paulian 1953 cited by Petter and Peyrieras 1972), where the male was slightly more rufous dorsally than a typical *P. coronatus*, and the female heavily black on the head, upper back, arms, hands, and ventrally, and grey on the nape base, lower back and tail. Given the lack of a precise location, however, it is difficult to interpret this observation in more detail. Further research into chromatic variation in *P. deckenii* and *P. coronatus* in western central Madagascar is clearly required to resolve this issue, and to better understand the distributions of the two taxa and their history of gene exchange.

Distribution of other species observed during the surveys

Our observations of *P. verreauxi* at two sites in the Amoron'i Mania Region confirm two previous observations of the species in the Region, made in the Itremo protected area (Wilmé *et al.* 2006; Wilmé and Callmander 2006). The

Mania River therefore appears to represent the distributional limit between this species and *P. coronatus* to the north (Razafindramanana and Rasamimanana 2010; Fig. 1). Our observations of *P. coquereli* at the Betonendry/Maroakanga site in the Betsiboka Region represent a southern extension of 90 km to the known range of the species (Fig. 1; Wilmé *et al.* 2006; Mittermeier *et al.* 2008, 2010). As with all other records of the species, the site is located to the east of the Betsiboka River (Fig. 1). The *P. verreauxi* and *P. coquereli* we observed were of typical coloration for their respective species (Fig. 4).

Our observation of two groups of *Eulemur mongoz* at the Anoboazo site in the Boeny Region represents a new location for this species, listed as Vulnerable on the IUCN Red List (IUCN 2012). The site is within the known species range (Mittermeier *et al.* 2010). Conversely, our observation of *Eulemur rufus* at the Ikey site in the Betsiboka Region appears to represent a small range extension for this species. Although Mittermeier *et al.* (2010) state that the species only occurs south and west of the Mahavavy River, there are several reported sites north and east of this river, west of the Betsiboka River (Wilmé *et al.* 2006). The Ikey site is 60 km south-east of the closest previously published site of Madirovalo in the Boeny Region (Rasoloharijaona *et al.* 2005; Wilmé *et al.* 2006), and 70 km east of the Kasijy Special Reserve, the closest site illustrated on the distribution map in Mittermeier *et al.* (2010).

Conservation implications for *P. coronatus*

Although *P. coronatus* may now be considered widely distributed through western central Madagascar, forest cover is very limited throughout most of its range, and most forests are small and fragmented. Any sifaka populations remaining in such fragmented forests are highly endangered due to anthropogenic threats such as hunting and habitat loss or degradation (Table 5), and to demographic influences related to small population sizes and isolation from other populations (Gilpin and Soulé 1986; Frankham 2005). Although the mean group size of *P. coronatus* we observed was almost the same as that observed by Pichon *et al.* (2010) in the relatively large population at Antrema, and larger than that given by Salmona *et al.* (this issue) elsewhere in the north of the species range, we encountered only one to five groups per survey site. The duration of our surveys was very limited at each site, and we therefore almost certainly overlooked some groups, but the available habitat at each site was very restricted, and population sizes are surely very low. We have therefore initiated further surveys at each of the seven new *P. coronatus* sites we report here, to obtain more accurate measures of population densities and habitat parameters, to collect fecal samples for genetic analysis, and to identify more specific conservation priorities. We recommend that conservation priorities include various aspects such as collaborative research to refine our knowledge of sifaka distribution, taxonomy, and chromatic variation, local education programs, socioeconomic development projects, facilitation of law enforcement efforts, and the creation and management of conservation zones that ensure

the maintenance of the full range of chromatic and genetic diversity of *P. coronatus*.

Acknowledgments

We thank the Environment and Forests Ministry of the government of Madagascar, represented by the Regional Directions of Bongolava, Betsiboka and Boeny, for their permission to undertake this research. We also thank all the traditional and administrative authorities of the zones we visited, the rural communes, fokontany, Gendarme, and local guides, porters and cooks, for their generous collaboration during this study. We thank Christelle Chamberlan, Mohamad Mbaraka, Rose Marie Randrianarison and Maholy Ravaloharimanitra for their help in organizing the study; and Lounès Chikhi and Urs Thalmann for their excellent reviews of the paper. The survey was financed by The Aspinall Foundation, within the framework of their Tsibahaka project for the conservation of the crowned sifaka.

Literature cited

- Blair, M. E., E. J. Sterling and M. M. Hurley. 2011. Taxonomy and conservation of Vietnam's primates: a review. *Am. J. Primatol.* 73: 1093–1106.
- Pichon, C., R. Ramanamisata, 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: 42–46.
- Curtis, D. J., A. Velo, E.-O. Raheliarisoa, A. Zaramody and P. Müller. 1998. Surveys on *Propithecus verreauxi deckeni*, a melanistic variant, and *P. v. coronatus* in northwest Madagascar. *Oryx* 32: 157–164.
- Frankham, R. 2005. Genetics and extinction. *Biol. Conserv.* 126: 131–140.
- Gilpin, M. E. and M. E. Soulé. 1986. Minimum viable populations: processes of species extinction. In: *Conservation Biology: The Science of Scarcity and Diversity*, M. E. Soulé (ed.), pp.19–34. Sinauer Associates, Sunderland, MA.
- Groves, C. P. and K. M. Helgen. 2007. Craniodental characters in the taxonomy of *Propithecus*. *Int. J. Primatol.* 28: 1363–1383.
- Hill, W. C. O. 1953. *Primates: Comparative Anatomy and Taxonomy I. Strepsirhini*. Edinburgh University Press, Edinburgh.
- IUCN. 2012. 2012 IUCN Red List of Threatened Species. International Union for Conservation of Nature (IUCN), Species Survival Commission (SSC), Gland, Switzerland and Cambridge, UK. Website: <<http://www.redlist.org>>.
- Milne-Edwards, A. and A. Grandidier. 1875. *L'histoire politique, physique et naturelle de Madagascar: Histoire naturelle des mammifères*. Imprimerie Nationale, Paris.
- Mittermeier, R. A., J. U. Ganzhorn, W. R. Konstant, K. Glander, I. Tattersall, C. P. Groves, A. B. Rylands, A. Hapke,

- J. Ratsimbazafy, M. I. Mayor, E. E. Louis Jr., Y. Rumpler, C. Schwitzer and R. M. Rasoloarison. 2008. Lemur diversity in Madagascar. *Int. J. Primatol.* 29: 1607–1656.
- Mittermeier, R. A., E. E. Louis Jr., M. Richardson, C. Schwitzer, O. Langrand, A. B. Rylands, F. Hawkins, S. Rajabellina, J. Ratsimbazafy, R. Rasoloarison, 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., A. Velo, E.-O. Rahelarisoa, A. Zaramody and D. J. Curtis. 2000. Surveys of five sympatric lemurs at Anjanena, northwest Madagascar. *Afr. J. Ecol.* 38: 248–257.
- Pastorini, J., M. R. J. Forstner and R. D. Martin. 2001. Phylogenetic history of sifakas (*Propithecus*: Lemuriformes) derived from mtDNA sequences. *Am. J. Primatol.* 53: 1–17.
- Petter, J.-J. 1969. Speciation in Madagascar lemurs. *Biol. J. Linn. Society* 1: 77–84.
- Petter, J.-J. and F. Andriatsarafara. 1987. Conservation status and distribution of lemurs in the west and northwest of Madagascar. *Primate Conserv.* (8): 169–171.
- Petter, J.-J. and A. Peyrieras. 1972. Melanization in the genus *Propithecus* Malagasy lemur. *J. Hum. Evol.* 1: 379–388.
- Petter, J.-J., R. Albignac and Y. Rumpler. 1977. *Mammifères Lémuriens (Primates Prosimiens)*. Faune de Madagascar 44: ORSTOM/CNRS, Paris.
- Rakotonirina, L., A. Rajaonson, T. Ratolojanahary, J. Rafalimandimby, P. Fanomezantsoa, B. Ramahefosa, T. Rasolofoharivelo, M. Ravaloharimanitra, J. Ratsimbazafy, R. Dolch and T. King. 2011. New distributional records and conservation implications for the critically endangered greater bamboo lemur *Prolemur simus*. *Folia Primatol.* 82(2): 118–129.
- Randrianarisoa, P. M., A. Rasamison and L. Rakotozafy. 2001a. Notes sur la faune lémurienne dans la Réserve Spéciale d’Ambohijanahary. *Lemur News* 6: 5.
- Randrianarisoa, P. M., A. Rasamison, L. Rakotozafy and A. Totovolahy. 2001b. Inventaire des lémuriens dans la Réserve Spéciale de Kasijy. *Lemur News* 6: 7–8.
- 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. B. Rasamimanana. 2010. Discovery of crowned sifaka (*Propithecus coronatus*) in Dabolava, Miandrivazo, Menabe Region. *Lemur News* 15: 23–25.
- Salmona, J., E. Rasolondraibe, F. Jan, A. Besolo, H. Rakotoarisoa, S. Viana Meyler, S. Wohlhauser, C. Rabarivola and L. Chikhi. this issue. Conservation Status and Abundance of the Crown Sifaka (*Propithecus coronatus*). *Primate Conserv.* this issue.
- Tattersall, I. 1982. *The Primates of Madagascar*. Columbia University Press, New York.
- Tattersall, I. 1986. Notes on the distribution and taxonomic status of some species of *Propithecus* in Madagascar. *Folia Primatol.* 46: 51–63.
- Tattersall, I. 1988. Distribution survey of the Malagasy lemurs: request for information and initial report. *Primate Conserv.* (9): 116–117.
- 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., T. Geissmann, A. Simona and T. Mutschler. 1993. The indris of Anjanaharibe-Sud, northeastern Madagascar. *Int. J. Primatol.* 14: 357–381.
- 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.
- The Aspinall Foundation 2009. Proposal for the creation of Projet Tsibahaka: Conservation of the Crowned Sifaka *Propithecus coronatus*. The Aspinall Foundation, Antananarivo, Madagascar. 5pp.
- The Aspinall Foundation 2010. Projet Tsibahaka: Conserving the Crowned Sifaka *Propithecus coronatus* – Initial results. Report, The Aspinall Foundation, Antananarivo, Madagascar. 10pp.
- Wilmé, L. and M. W. Callmander. 2006. Les populations reliques de primates: les Propithèques. *Lemur News* 11: 24–31.
- Wilmé, L., S. M. Goodman and J. U. Ganzhorn. 2006. Biogeographic evolution of Madagascar’s microendemic biota. *Science* 312: 1063–1065.
- Zaonarivelo J. R., R. Andriantompohavana, S. E. Engberg, S. G. Kelley, J.-C. Randriamanana, E. E. Louis Jr. and R. A. Breneman. 2007. Morphometric data for Indri (*Indri indri*) collected from ten forest fragments in eastern Madagascar. *Lemur News* 12: 17–21.

Authors’ addresses:

Laingoniaina H. F. Rakotonirina, Josia Razafindramanana, The Aspinall Foundation, BP 7170 Andravoahangy, Antananarivo 101, Madagascar, and Groupe d’Etude et de Recherche sur les Primates de Madagascar (GERP), Lot 34 Cité des Professeurs Fort Duchesne, Ankatso, Antananarivo 101, Madagascar. E-mail of the first author: <laingoniaina2000@yahoo.fr>, **Fetraharimalala Randriantsara**, **Andoniaina H. Rakotoarisoa**, **Rado Rakotondrabe**, **Jonah Ratsimbazafy**, Groupe d’Etude et de Recherche sur les Primates de Madagascar (GERP), Lot 34 Cité des Professeurs Fort Duchesne, Ankatso, Antananarivo 101, Madagascar. E-mail: <gerp@moov.mg>, **Tony King**, The Aspinall Foundation, BP 7170 Andravoahangy, Antananarivo 101, Madagascar. E-mail: <tonyk@aspinallfoundation.org>.

Received for publication: November 2011

Revised: February 2013