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Distributional Limits and Melanism in the South-west of the Range of the Crowned Sifaka (*Propithecus coronatus*), Madagascar

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Abstract: From mid-November to late December 2011, we surveyed 12 sites in nine communes in and around the south-western part of the range of the Endangered crowned sifaka *Propithecus coronatus* in western Madagascar. We observed sifaka appearing to be *P. coronatus* at four sites in the Menabe Region; at three of them several of the sifaka were melanistic. Decken's sifaka *P. deckenii* were recorded at three sites, and Verreaux's sifaka *P. verreauxi* at one site. We found no evidence of sifakas between the Tsiribihina and Manambolo rivers west of latitude about 45°E, and local people claimed they have never existed there. We therefore recommend that the forests in this area be excluded from the current distribution range of *P. coronatus*. We found no sifakas resembling *P. deckenii* in the melanistic *P. coronatus* groups, which appears to confirm the hypothesis that most previous reports of possible sympatry between these two species can be better explained by melanism in *P. deckenii*. The typical individuals of *P. coronatus* we report showed lightly or heavily washed rufous coloration on the forearms and upper back. The melanistic forms we describe can be categorized as either a "very dark" form, characterized by dark brown to blackish coloration on the forearms and upper back, or as an "intermediate" form, showing dull rufous or light brown forearms and upper back. In reality there appeared to be a continuum in chromatic variation from the typically colored individuals, through the intermediate melanistic form, to the very dark form. These melanistic sifakas appear similar to the darker melanistic forms of *P. deckenii* north of the Manombolo River, rather than to the melanistic forms of *P. coronatus* reported to the south-east of our survey sites, or to melanistic forms of *P. verreauxi* south of the Tsiribihina River. Ancient gene-flow between sifaka taxa may be one of the causes of these melanistic tendencies, but we recommend further research to clarify the situation. These newly reported populations are at a high risk of local extinction. Containing melanistic forms not found elsewhere, we propose that they should be considered of considerable conservation importance with regard to preserving unique chromatic variation, and probably also genetic diversity, in *P. coronatus*.

Key words: *Propithecus coronatus, Propithecus deckenii, Propithecus verreauxi*, gene flow, melanism

Introduction

The crowned sifaka *Propithecus coronatus* is an Endangered (IUCN 2012; Salmona *et al.* 2014) lemur endemic to Madagascar. Recent work has led to a greatly improved understanding of its distribution (King *et al.* 2012; Rakotonirina *et al.* 2014) and abundance (Salmona *et al.* 2014). However, while the distribution of the species is fairly clear in the northern part of its range, where it is limited to remaining dry deciduous forest fragments between the Betsiboka and Mahavavy rivers, it is less clear in the southern parts (Mittermeier *et al.* 2008, 2010; Rakotonirina *et al.* 2014). Rakotonirina *et al.* (2014) therefore recommended further surveys to refine the known limits of the species in the south-west of its range, between the Mahajilo, Manambolo and Tsiribihina rivers (Figs. 1 and 2). This same region is also important for investigating patterns of sifaka chromatic variation and melanism, with melanistic sifaka occurring to the north of the Manambolo River within populations of Decken's sifaka *P. deckenii* (Petter and Peyrieras 1972; Petter *et al.* 1977; Tattersall 1986; Curtis *et al.* 1998; Thalmann *et al.* 2002; Rakotonirina *et al.* 2014), to the south of the Mahajilo River in a group of crowned sifaka (Razafindramanana and Rasamimanana 2010; Rakotonirina *et al.* 2014), and to the south of the Tsiribihina River in populations of Verreaux's sifaka *P. verreauxi* (Mittermeier *et al.* 2010). Defining species distributions is important for conservation decision-making (Anderson and Martınez-Meyer 2004; Thorn *et al.* 2009; Rakotonirina *et al.* 2011), and understanding variation within a species distribution can help define what needs to be conserved (Blair *et al.* 2011).

With the aim of contributing to a species conservation project for the crowned sifaka (The Aspinall Foundation 2009, 2010; King *et al.* 2012; Rakotonirina *et al.* 2014), we therefore undertook a survey of the south-west part of the crowned sifaka range in late 2011. Here we present the results of this survey, including newly reported sites supporting sifakas, descriptions and photographs of chromatic variation amongst the sifaka populations, and preliminary assessments of the threats facing the sites.

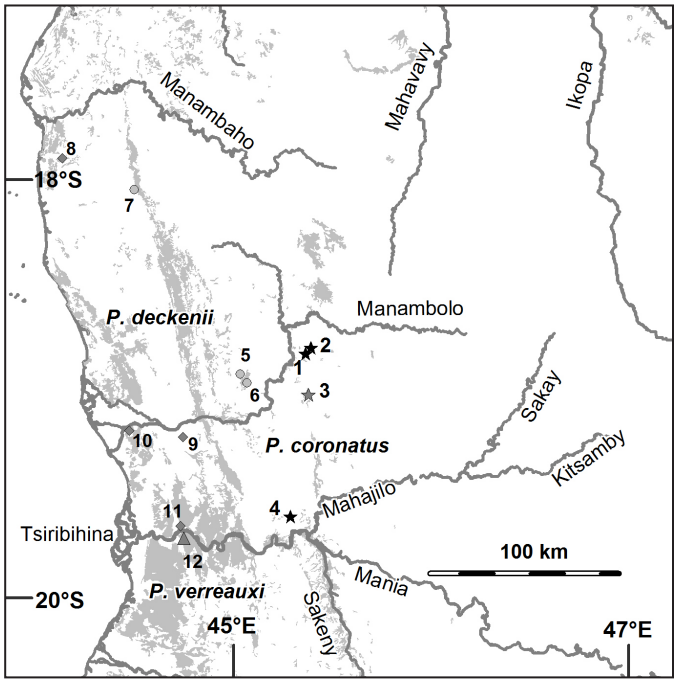

Figure 1. Map of the study site in western Madagascar showing major rivers (dark gray), approximate forest cover (light gray), and survey sites (numbered symbols) where we observed typical *P. coronatus* only (gray stars), *P. coronatus* occurring with melanistic forms (black stars), *P. deckenii* (circles), *P. verreauxi* (triangles), or an absence of sifakas (diamonds). The names of our numbered survey sites are: 1-Marolaka; 2-Ankaboka; 3-Itondy; 4-Bekopaka; 5-Bevinoa; 6-Antsakavirohazo; 7-Beanka; 8-Andrea; 9-Ankoadava; 10-Ankitapo; 11-Masoarivo; 12-Ambalakapoaky.

Methods

From mid November to late December 2011, two of us (L. Rakotonirina and A. Rakotoarisoa) surveyed 10 sites in seven communes of the Menabe Region of western Madagascar, and an extra two sites in the Melaky Region (Table 1; Fig. 1). Ten of the survey sites were at low elevation (12 to 261 m above sea level), the other two were at low to middle elevations (189 to 780 m above sea level). This area comprises large areas of wooded grassland-bushland mosaics, with restricted areas of fragmented western dry forest, sometimes as gallery forest along watercourses (Moat and Smith 2007).

Following similar methods to those used in previous surveys (Rakotonirina *et al.* 2014), we consulted local authorities and local populations to select the sites for surveying. We surveyed the sites for one to three days each (Table 1). Accompanied by local guides, we searched for sifakas following paths in the forest or by walking along the edge of forest patches or gallery forests. On each occasion that we observed sifakas 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 evidence of threats to the sites. Lemur nomenclature follows Mittermeier *et al.* (2010).

Results

We made direct observations of sifaka at eight of the 12 survey sites (Table 1; Fig. 1). We observed sifaka appearing to be *P. coronatus* at four sites, at three of which several of the sifaka were melanistic (Tables 1, 2; Fig. 1). We found *P. deckenii* at three sites, and *P. verreauxi* at one site (Tables 1, 2; Fig. 1). Sifaka appeared to be absent at the four remaining sites (Table 1), including at the three sites in the relatively

Table 1. Sites surveyed during 2011, summarizing the main results for the presence of sifaka.

Region	Commune	Site	Notes	Survey Dates	Coordinates	Altitude (m)
Sites with *P. coronatus*						
Menabe	Ankavandra	Marolaka	1 group, incl. melanistic	2 Dec	18.831°S 45.363°E	189–497
Menabe	Ankavandra	Ankaboka	2 groups, 1 incl. melanistic	2 Dec	18.803°S 45.390°E	756–780
Menabe	Itondy	Itondy	1 group, not melanistic	6 Dec	19.020°S 45.380°E	137–147
Menabe	Bemahatazana	Bekopaka	1 group, incl. melanistic	28 Dec	19.611°S 45.288°E	61–85
Sites with *P. deckenii*						
Menabe	Ankavandra	Bevinoa	2 groups	24–26 Nov	18.930°S 45.033°E	148–223
Menabe	Ankavandra	Antsakavirohazo	3 groups	26–27 Nov	18.965°S 45.066°E	178–261
Melaky	Belitsaka	Beanka	1 group	9 Dec	18.046°S 44.498°E	252
Sites with other species, or no sifaka were found						
Melaky	Andrea	Andrea	Sifaka apparently absent	15 Dec	17.897°S 44.133°E	26–39
Menabe	Andimaky Manambolo	Ankoadava	Sifaka apparently absent	18–19 Dec	19.230°S 44.745°E	47–51
Menabe	Amboalimena	Ankitapo	Sifaka apparently absent	19 Dec	19.187°S 44.458°E	28
Menabe	Masoarivo	Masoarivo	Sifaka apparently absent	23 Dec	19.656°S 44.733°E	23
Menabe	Tsimafana	Ambalakapoaky	*P. verreauxi* (1 group)	21 Dec	19.716°S 44.750°E	12–67

forested part of the survey area between the Tsiribihina and Manambolo rivers (Fig. 1). We recorded no other species of lemur during the surveys.

The *P. deckenii* individuals we observed (Fig. 3) were of typical coloration, as described by Mittermeier *et al.* (2010) and Rakotonirina *et al.* (2014). The three *P. verreauxi* individuals we observed were also of generally typical coloration for the species, although one showed a quite dark brownish patch covering much of its back (Fig. 3).

At the four sites where we recorded *P. coronatus*, 56% of individuals we saw (nine of 16) had typical *P. coronatus* coloration (Table 2; Fig. 4). The other 44% (seven individuals, including two infants) showed melanistic tendencies (Table 2; Figs. 5, 6). Two of five groups contained only typical individuals, the three other groups contained both typical and melanistic individuals (Table 2). The two infants we observed were melanistic, and both were carried by melanistic adults (Table 2; Fig. 5).

The typical individuals showed lightly or heavily washed rufous coloration on the forearms and upper back (Table 3; Figs. 4–6). For the purposes of describing the chromatic variation we recognized two melanistic forms, a "very dark" form characterized by dark brown to blackish coloration on the forearms and upper back, and an "intermediate" form with dull rufous or light brown forearms and upper back (Table 3; Figs. 5 and 6). In reality there appeared to be a continuum in chromatic variation from the typically colored individuals, through the intermediate melanistic form to the very dark form.

The sizes of *P. coronatus* groups we observed ranged from one to five individuals (Table 2; mean = 3.2, SD = 1.48, n = 5), and of groups of *P. deckenii* from two to five individuals (Table 2; mean = 3.5, SD = 1.05, n = 6).

We noted the presence of various threats to the sifakas and their habitat at each of the eight sites where sifakas were

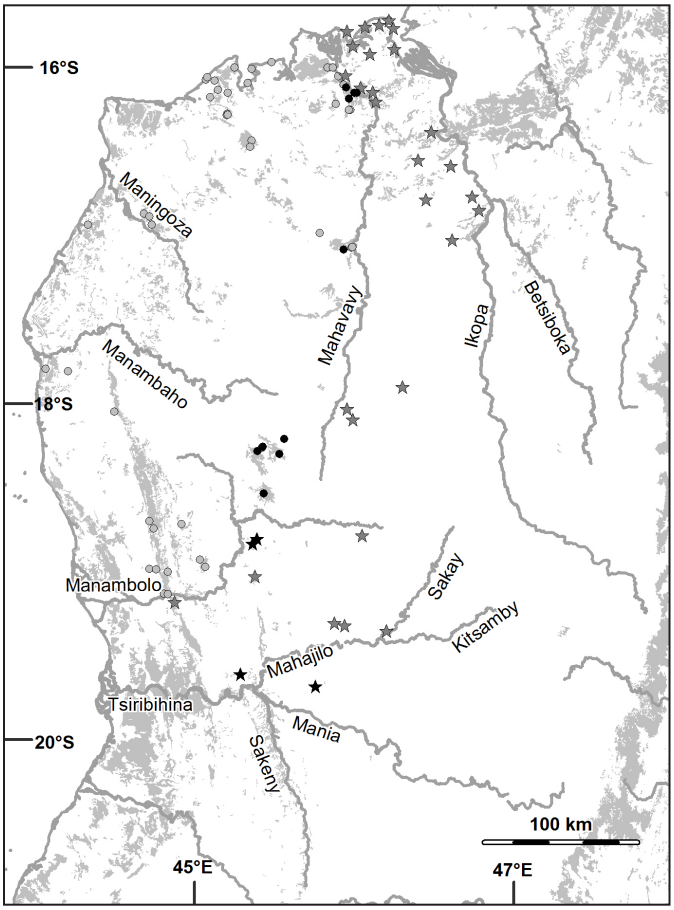

Figure 2. Map of west and western central Madagascar showing major rivers (dark gray), approximate forest cover (light gray), distributional records of *P. coronatus* (gray stars), *P. deckenii* (gray circles), *P. coronatus* occurring sympatrically with melanistic forms (black stars) and *P. deckenii* occurring sympatrically with melanistic forms (black circles). 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). Distribution records are taken from Wilmé *et al.* (2006) and references therein, Tattersall (1986), Thalmann and Rakotoarison (1994), Razafindramanana and Rasamimanana (2010), King *et al.* (2012), Rakotonirina *et al.* (2014), Salmona *et al.* (2014), and this paper.

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

Site	Locality[a]	Date	Latitude	Longitude	Altitude (m)	Group size	Infants	Melanistic
Sites with *P. coronatus*								
Marolaka	Andohanimarolaka	02/12/2011	-18.832	45.364	489	3	1[b]	2
Ankaboka	Ambalan'i Georges	02/12/2011	-18.803	45.390	756	1	0	0
Ankaboka	Ambalan'i Georges	02/12/2011	-18.804	45.390	780	4	1[b]	2
Itondy	Ankily ambany	06/12/2011	-19.027	45.379	147	3	0	0
Bekopaka	Bekopaka	28/12/2011	-19.611	45.288	85	5	0	3
Sites with *P. deckenii*								
Bevinoa	Mativoly	24/11/2011	-18.929	45.033	205	2	0	0
Bevinoa	Mativoly	25/11/2011	-18.930	45.032	207	3	0	0
Antsakavirohazo	Andovoka	26/11/2011	-18.947	45.061	219	5	1	0
Antsakavirohazo	Angora	27/11/2011	-18.971	45.069	185	4	0	0
Antsakavirohazo	Antsalova	27/11/2011	-18.975	45.060	178	4	0	0
Beanka	Beanka Ambinda	09/12/2011	-18.046	44.498	252	3	0	0
Sites with *P. verreauxi*								
Ambalakapoaky	Analamay / Tsinjorano	21/12/2011	-19.716	44.750	63	3	0	0

[a] We use the term "locality" to describe specific forest fragments or other locally-named locations within our main survey sites
[b] Melanistic infant with melanistic adult

Table 3. Chromatic description of *P. coronatus* and melanistic forms observed at the sites of Marolaka, Ankaboka, Itondy and Bekopaka, in the Menabe Region of western Madagascar, December 2011.

Form	Head	Nape	Back	Outer surface of arms	Outer surface of legs	Chest and abdomen	Tail	Root of tail
Typical *P. coronatus*	Black, dark brown or with reddish tinge; in one case rufous cap	Whitish	Lightly or heavily washed rufous in the upper half, whitish lower half	Light or dark rufous	Whitish, some with rufous on thigh	Dark brown / rufous	Whitish	Whitish or light rufous
Melanistic 1 (intermediate)	Black or dark brown	Gray or brown	Dull rufous or brown on upper half, light gray on lower half	Brown on anterior and whitish on posterior aspects	Light rufous or brown on anterior aspect of thigh, whitish elsewhere	Dark brown / rufous	Whitish, light gray or light rufous	Whitish or grayish
Melanistic 2 (very dark)	Black or dark brown	Light gray to dark brown	Black or very dark brown on upper half, light gray on lower half	Black or very dark brown on anterior aspect, grayish on posterior aspect	Light rufous or gray on anterior aspect of thigh, whitish elsewhere	Dark brown	Whitish, light gray or light rufous	Whitish or grayish

Figure 3. A typical *P. deckenii* at the Bevinoa survey site (left), and a *P. verreauxi* showing a fairly dark back at the Ambalakapoaky survey site. Photographs by L. Rakotonirina.

Figure 4. Sifaka at the Itondy survey site, showing typical *P. coronatus* coloration. Photographs by L. Rakotonirina.

seen (Table 4). With the notable exception of the Beanka site, where we noted significant disturbance only near the major road running through it, all the sites had several threats, particularly related to habitat disturbance and fragmentation (Table 4). There was logging at two sites, and hunting pressure was high at five sites (Table 4).

Discussion

Geographic range of P. coronatus

Whilst our observations of *Propithecus deckenii* and *P. verreauxi* are unremarkable, occurring within the known ranges for the two species as given by Mittermeier *et al.* (2010), our observations of *P. coronatus* at four newly reported sites in the Menabe Region, and of an absence of sifakas at three sites in the western parts of this region, help to resolve the confusion over sifaka species limits in the south-west of the *P. coronatus* range, especially between the Mahajilo, Manambolo and Tsiribihina rivers (Rakotonirina *et al.* 2014; Fig. 2).

The three most northerly *P. coronatus* sites we report here, in the Ankavandra and Itondy communes, confirm that the Manambolo River is a boundary between the current distributions of *P. coronatus* and *P. deckenii*, even in its upper reaches (Fig. 2). More significantly, our results suggest an absence of sifakas between the Tsiribihina and Manambolo rivers west of latitude about 45°E (Figs. 1, 2). We found no evidence of sifakas in this region, and local people claimed they have never existed there. Indeed the Sakalava people native to the area consider the potential sighting of sifakas in this area as a malediction. With only one, non-georeferenced, published observation of *P. coronatus* in this general area (Thalmann and Rakotoarison 1994, which also included a single *P. deckenii*), and one puzzling observation of *P. verreauxi* lacking detail or explication (Zicoma 1998 in Wilmé *et al.* 2006), we recommend that the forests in this area be excluded from the current distribution range of *P. coronatus*. According to the forest cover data gathered from satellite images in 1999 and 2000 by the Madagascar Vegetation Mapping Project data (Moat and Smith 2007), this area includes approximately 1,300 km² of forests, therefore representing over 30% of the forest cover included in the total range of *P. coronatus* as proposed by Salmona *et al.* (2014) when estimating potential total population size for the species. Total forest cover in the range of *P. coronatus* is therefore probably between 1,600 and 2,850 km², rather than the 2,350 to 4,150 km² suggested by Salmona *et al.* (2014) based on the differing vegetation cover data-sets of MEFT-USAID-CI (2009) and Moat and Smith (2007) respectively. This would consequently have an impact on the total population estimates for *P. coronatus* given by Salmona *et al.* (2014), but would not alter the IUCN Red List category they propose of Endangered B1ab.

Melanism in P. coronatus

Our descriptions and photographs of melanistic individuals from three of the *P. coronatus* sites we report here add significantly to our knowledge of melanism in this species (King *et al.* 2012), which in most of its range exhibits fairly limited chromatic variation (Milne-Edwards and Grandidier 1875; Petter and Peyrieras 1972; Rakotonirina *et al.* 2014), with a general tendency of increasing rufous coloration on the back and limbs from the north to the south of its distribution (Rakotonirina *et al.* 2014). Melanism in *P. coronatus* had previously only been reported from a pair captured at an unspecified location "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 was heavily black on the head, upper back, arms, hands, and ventrally, and gray on the base of the nape, the lower back and tail, and from the most southerly known *P. coronatus* site of Dabolava, where

Table 4. Threats observed at each of the survey sites where we observed sifaka. (+++: severe; ++: frequent; +: occasional).

	Marolaka	**Ankaboka**	**Itondy**	**Bekopaka**	**Bevinoa**	**Antsakavirohazo**	**Beanka**	**Ambalakapoaky**
Sifaka species present	*P. coronatus*	*P. coronatus*	*P. coronatus*	*P. coronatus*	*P. deckenii*	*P. deckenii*	*P. deckenii*	*P. verreauxi*
Hunting	+++	+++	+++	+	+++	+++		+
Logging			+++					+++
Tree cutting for local use	+++	+++	+++	++	+++	+++		+++
Charcoal production	+++	+++	+++	++	+++	+++		+++
Forest fires	+++	+++	+++	++	+++	+++		+++
General human activity	+++	+++	+++	+++	+++	+++		+++
Disturbance by cattle	++	++	++	++	++	++		++
Disturbance due to major road							+++	
Forest fragmentation	+++	+++	+++	++		+++		+++
Official zonation status	none	none	none	none	none	none	protected area	new protected area

some individuals show varying degrees of dark blackish patches on their shoulders, mid-back, and upper aspects of their arms and thighs (Razafindramanana and Rasamimanana 2010; Rakotonirina *et al.* 2014).

The presence of a large proportion of melanistic sifakas in the *P. coronatus* groups at the two sites we report in the Ankavandra commune, south of the Manambolo river but only 30 km south of *P. deckenii* populations to the north of the Manambolo containing melanistic sifakas (Randrianarisoa *et al.* 2001; Thalmann *et al.* 2002; Rakotonirina *et al.* 2014; Fig. 2), suggests that the melanistic tendencies in both species may be related to former gene flow between them, perhaps during periods of increased habitat connectivity. Other potential causes of melanism in several sifaka species have been proposed, including intermediate environmental or climatic conditions leading to reduced selection pressures and increased expression of variation (Petter and Peyrieras 1972; Petter *et al.* 1977), but occasional gene flow seems the most likely explanation (Thalmann *et al.* 2002; King *et al.* 2012), perhaps accentuated by intermediate environmental or climatic conditions.

Our observation of melanism in *P. coronatus* at the Bekopaka site in the Bemahatazana Commune, in gallery forest along a minor northern tributary of the Tsiribihina River, is intriguing as the site is closer to the range of *P. verreauxi* to the south of the Tsiribihina than to the range of *P. deckenii*. However, the melanistic sifakas at the site (Fig. 6) appear similar to those in the *P. coronatus* groups in the Ankavandra commune further north (Fig. 5), and to the darker melanistic forms of *P. deckenii* north of the Manombolo (Rakotonirina *et al.* 2014), rather than to melanistic forms of *P. verreauxi* (Mittermeier *et al.* 2010, pp. 526–527). Interestingly, some of the *P. coronatus* individuals at Dabolava, only 50 km east of Bekopaka but south of the Mahajilo River (a major tributary of the Tsiribihina) show melanistic tendencies similar to those expressed by *P. verreauxi*, of dark blackish patches on the shoulders and limbs (Fig. 7; Razafindramanana and Rasamimanana 2010; Rakotonirina *et al.* 2014), rather than those expressed at the *P. coronatus* sites we report here, or at *P. deckenii* sites. The implication is perhaps that melanism in *P. coronatus* at Dabolava may be linked to former gene flow with *P. verreauxi*, whilst at sites between the Tsiribihina and

Figure 5. Chromatic variation of *P. coronatus* at the Marolaka and Ankaboka survey sites, Ankavandra Commune, including typical *P. coronatus* individuals (top left and center), an individual with an unusual rufous cap (top right), and various melanistic forms (bottom line). Photographs by L. Rakotonirina.

Manambolo rivers it may be linked to former gene flow with *P. deckenii*.

The precise mechanisms by which gene flow might lead to melanistic tendencies in sifakas remain unclear, especially as melanistic forms do not often resemble first-generation hybrids (Petter and Peyrieras 1972; Petter *et al.* 1977; Rakotonirina *et al.* 2014). However melanin-based pigmentation, the most frequent form of pigmentation in primate skin and hair, is known to be genetically controlled (Bradley and Mundy 2008). Two pigmentation genes important in melanin synthesis, the melanocortin-1 receptor (MC1R) and agouti signaling protein (ASIP), have been identified as having a major contribution to chromatic variation in a wide number of animals (Hubbard *et al.* 2010), although their role in primate coat color variation is complex (Mundy and Kelly 2003, 2006; Bradley and Mundy 2008). Ancestral polymorphism in such pigmentation genes across the *Propithecus* genus might be one plausible explanation for increased chromatic variation in sifaka populations subject to inter-taxa gene-flow. Again, we recommend further research, including genetic analysis, into the factors influencing chromatically variable sifaka populations throughout Madagascar (Rakotonirina *et al.* 2014; Fig. 8).

Another interesting observation is that we found no sifakas resembling *P. deckenii* in the melanistic *P. coronatus* groups. This appears to confirm our previous hypothesis that most previous reports of possible sympatry between these two species can better be explained by melanism in *P. deckenii*, where some "intermediate" melanistic forms resemble *P. coronatus* (Rakotonirina *et al.* 2014). Any significant gene flow between the two species is therefore likely to be ancient rather than current. Confirmed observations of the species occurring together (Tattersall 1982, 1988; Thalmann and Rakotoarison 1994; Thalmann *et al.* 2002) are rare, involve only one or two individuals of one species amongst larger numbers of the other, and can be plausibly explained by local and infrequent (perhaps including human-assisted) crossing of biogeographical barriers (Rakotonirina *et al.* 2014), with minimal subsequent gene flow. Despite the distinctive cranial features of *P. coronatus* museum specimens (Groves and Helgen 2007),

Figure 6. Sifaka at the Bekopaka survey site, Bemahatazana Commune, including typical *P. coronatus* individuals (top left), and melanistic forms. Photographs by L. Rakotonirina.

the lack of sympatry, probable former gene flow leading to melanistic tendencies, the potential to hybridize (Petter 1969), and the lack of genetic differentiation (Rumpler *et al.* 2011), all add weight to the argument that recognizing *P. coronatus* and *P. deckenii* as full species might be regarded as a case of taxonomic inflation (Tattersall 2007, 2013).

Threats and conservation

The sifaka group sizes we recorded during this survey were generally similar to those recorded for these species elsewhere (Pichon *et al.* 2010; King *et al.* 2012; Rakotonirina *et al.* 2014; Salmona *et al.* 2014), but six of the eight sites where we found sifakas contained limited and highly fragmented forest cover, including all four of the sites where we observed *P. coronatus* (Table 4). Coupled with severe hunting pressure at most sites, other anthropogenic threats (Table 4), and demographic factors influencing small isolated populations (Gilpin and Soulé 1986; Frankham 2005), these newly reported populations are at a high risk of local extinction. The number of sifakas at these isolated sites is probably only a small fraction of the total wild population of *P. coronatus* (Salmona *et al.* 2014). However, the populations contain melanistic forms not found elsewhere, and as such should be considered of considerable conservation importance in terms of preserving unique chromatic variation, and probably also genetic diversity, within *P. coronatus*. We therefore reiterate our previous recommendation (Rakotonirina *et al.* 2014) to facilitate the creation and management of conservation zones that ensure the maintenance of the full range of chromatic and genetic diversity of *P. coronatus*.

Figure 7. Melanistic forms of *P. coronatus* at Dabolava, near Miandrivazo, in May 2010. Photographs by F.-G. Grandin / MNHN.

Figure 8. A pale form of *P. verreauxi* with a white rather than brown cap at Berenty private reserve, southern Madagascar, in October 2010 (left); a melanistic form of *P. deckenii* at Orimbato, near Ambohijanahary Special Reserve, in March 2010 (center; see Rakotonirina *et al.* 2014), and two melanistic female sifaka currently in the American Museum of Natural History and collected by A. L. Rand and R. Archbold at "Ambararatabe; Soalala" on 30 March 1931 (right; see Tattersall 1986). Photographs by T. King (left), L. Rakotonirina (center) and Jen Crick / AMNH (right).

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