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With a Special Section on the Crowned Sifaka (*Propithecus coronatus*)

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**Front cover:** Adult female eastern patas monkey *Erythrocebus patas pyrrhonotus*, Laikipia County, central Kenya. The patas monkey is a highly threatened species in Kenya. See pages 117–128 in this issue for more information on the primates of Laikipia and their conservation. Photograph by Yvonne de Jong and Tom Butynski.

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# Contents

## Neotropical Region

## Madagascar

# Africa

# Asia

# Obituaries

*Primate Conservation* 2014 (28): 1–8

# Diversity, Abundance and Habitats of the Primates in the Río Curaray Basin, Peruvian Amazonia

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**Abstract:** Western Amazonia is one of the regions of the world with the highest terrestrial biodiversity. We conducted transect censuses between November and December 2012 in order to determine the diversity and the densities of primate populations, and their group sizes and habitat use in the Río Curaray region. During 610 km of transect surveys, we encountered 304 groups of 13 primate species. Woolly monkeys, *Lagothrix poeppigii*, were the most frequently observed (n = 49 sightings) and pygmy marmosets, *Cebuella pygmaea*, the least (n = 8). Population density was lowest for howler monkeys, *Alouatta seniculus* (9.8 individuals km$^{-2}$) and saki monkeys, *Pithecia aequatorialis* (11.8 individuals km$^{-2}$) and highest for squirrel monkeys, *Saimiri macrodon* (65.0 individuals km$^{-2}$) and woolly monkeys (65.3 individuals km$^{-2}$). Primate groups were most frequently encountered in "palmales de altura" (97 encounters of 12 species). In conclusion, the Río Curaray region harbors a very high diversity of primates, matching other sites in Amazonia and worldwide, and populations there are evidently healthy and well conserved. We recommend the creation of a protected area contiguous with the Yasuní National Park in Ecuador.

**Key Words:** Western Amazonia, primate diversity, population density, habitat

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## Introduction

Amazonia, particularly its western part, is one of the most species-rich regions of the world (for example, Gentry 1988; Voss and Emmons 1996; Myers *et al.* 2000). The Río Napo, a major tributary of the upper Río Amazonas, has been identified as a center of species richness for four major taxa—vascular plants, amphibians, birds, and mammals (Bass *et al.* 2010)—indicating the importance of this region for global, regional and local conservation efforts. However, the forests there are coming under increasing threat, particularly due to oil and gas exploration and drilling (Finer *et al.* 2008; Soto *et al.* 2010). Like other areas in Peru, the Río Napo region is part of the country-wide concessions for oil drilling (Perú Petro 2007); a continuously growing threat to habitats and species. Primates, particularly the larger species of the family Atelidae, are sensitive to habitat disturbance and fragmentation (Cowlishaw and Dunbar 2000). Even small-scale disturbance such as seismic explorations preceding actual oil drilling may affect their populations (Kolowski and Alonso 2012). Furthermore, bushmeat hunting, which often increases when remote areas become more accessible due to commercial, large-scale exploitation of oil, gas and timber, is also a major threat to primate populations in Amazonia (Peres 1990).

With this background, we conducted a survey of primate populations along the upper Río Curaray, a southern tributary of the Río Napo. This is a relatively remote area (300 km from the city of Iquitos) but may become a focus of oil exploitation. Although a few general or taxon-specific primate surveys have been conducted in the Río Curaray basin (Aquino *et al.* 2005, 2013; Heymann 2000; Heymann *et al.* 2002; Kolowski and Alonso 2012), the status of the primate fauna of this area is little known.

Here we present the results of a survey conducted in November and December 2012 on both banks of the upper Río Curaray. We were interested in evaluating the diversity and abundance of primate populations and their relationship to habitat type, and examining whether this river is a species boundary in its upper reaches, as suggested by previous studies on *Saguinus* and *Pithecia* (Heymann *et al.* 2002; Aquino *et al.* 2009a).

## Methods

### *Study area*

The Río Curaray is in the extreme northwest of Peruvian Amazonia, towards the border with Ecuador, and is included in Lote 39 of the oil drilling concession to Repsol Exploración Perú (Perú Petro 2007). So far, forests along both sides of the Curaray show only slight disturbance, mainly due to sporadic logging and subsistence hunting. They will, however, be exposed to the threats emerging from petroleum prospecting and the infrastructure and personnel that accompany it.

Climate data from the nearest meteorological station (Arica, 1°36'01"S, 75°12'01"W, at the confluence of the ríos Nashiño and Curaray; Fig. 1) are available only for the period between December 1976 and July 1982 (SENAMHI 2008). Mean annual rainfall exceeds 2200 mm per year, with January receiving <150 mm per month.

For our censuses, we identified four different areas, two on each bank of the Curaray (Fig. 1; for geographic coordinates and habitat types see Table 1). We distinguished the following habitat types:

High forest (*monte alto*): vegetation composed almost entirely of trees of generally 20–25 m height, with some emergents above 30 m; open understorey, compact soils. Common tree species: *Macrolobium angustifolium* (Fabaceae; common name: "pashaco"), *Eschweilera* spp. (Lecythidaceae; "machimango"), *Couma macrocarpa* (Apocynaceae; "leche huayo"), *Chrysophyllum* spp. (Sapotaceae; "caimitillo"), *Cedrelinga cateniformis* (Fabaceae, "tornillo"), *Parahancornia* sp. (Apocynaceae; "naranjo podrido"), *Pouteria* spp. (Sapotaceae; "caimitillo"), *Hymenaea courbaril* (Fabaceae; "azúcar huayo") and *Vantanea* spp. (Humiriaceae; "añuje rumo"). The few palms (Arecaceae) are mainly *Astrocaryum murumuru* ("huicungo") and *Iriartea* sp. ("pona"). This vegetation type is common on low hills and high terraces.

Low forest (*monte bajo*): trees with heights of 15 to 20 m, the majority covered by epiphytes and lianas. Dense understorey characterized by the presence of herbaceous plants such as *Calathea* sp. (Marantaceae; "bijao"), *Bactris* sp. (Arecaceae; "ñejilla") and *Costus* sp. (Costaceae; "cañagria"); includes riparian vegetation. Common tree and liana species are *Couroupita guianensis* (Lecythidaceae; "ayahuma"), *Inga* spp. (Mimosaceae; "shimbillo"), *Cecropia* spp. (Cecropiaceae "cético"), *Rheedia* sp. (Clusiaceae; "charichuelo"), *Annona* sp. (Annonaceae; "anona") and *Passiflora* sp. (Passifloraceae; "granadilla"). This habitat type is common on low and medium terraces, and is subject to inundation on the lower terraces.

*Palmal de altura*: dominated by palms of 20–25 m height, intermingled with emergent trees of >30 m height such as *M. angustifolium* and *Eschweilera* spp. The most common palms are *Oenocarpus bataua* ("ungurahui"), *Socratea* sp. ("huacrapona"), *Iriartea* sp., *Astrocaryum chambira* ("chambira"), *A. murumuru*, *Phytelephas macrocarpa* ("yarina"), *Scheelea cephalotes* ("shapaja") and *Scheelea* sp. ("shebón"). The understorey is generally open and sometimes abundant in small *Lepidocaryum tenue* ("irapay") palms or perennial herbs. This habitat type is found mainly on low hills and high terraces.

*Palmal de planicie*: dominated (>70% of individuals) by *Mauritia flexuosa* (Arecaceae; "aguaje"), associated with *Mauritiella* sp. (Arecaceae; "aguajillo"), *Euterpe* sp. (Arecaceae; "chonta") and some fig trees *Ficus* (Moraceae; "renaco"). Common in medium and low terrace forests. Abundance of stilt roots and frequent flooding with black water

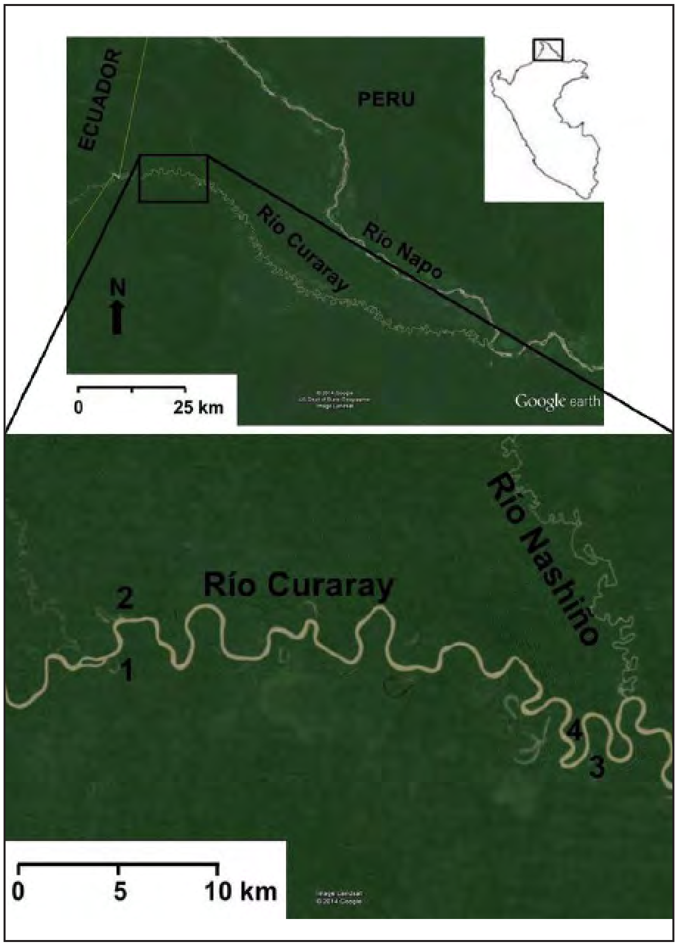

**Figure 1.** Location of survey sites on the Río Curaray. Numbers correspond to the list in Table 1.

**Table 1.** Census areas and their predominant forest types at the Río Curaray.

| Area | River bank | Coordinates | Name | Predominant forest types |
|---|---|---|---|---|
| 1 | Right | 452622/9829407 | Paujil | Medium and low terrace forest |
| 2 | Left | 474749/9821868 | Shuyal | High and low terrace forest |
| 3 | Right | 452080/9826841 | Colpa | High and low terrace forest |
| 4 | Left | 475731/9821084 | Ponal | Low hill forest, high and medium terrace forest |

can make access difficult. Subject to inundation on the low terraces.

*Varillal*: dense vegetation with trees and small trees between 10 and 25 m and few emergents above 30 m. Trees bolt upright with sclerophyllic leaves, similar to typical white-sand forests of the Peruvian Amazon. The soils differ from typical white-sand forest, however, by being sandy-clayey and rarely entirely sandy. Emergent trees represented mainly by *Parkia* spp., *Manilkara* spp. and *Eschweilera* spp. Uniquely present south of the Curaray in so-called *manchales*, located between peaks of the low hills, and on high terraces.

Tree swamp (*pantano arbóreo*): composed of trees of 20–25 m with an open understorey and ground covered by standing water and abundant stilt roots. The vegetation is dominated by *Ficus* spp. ("renaco"), intermingled with *Tachigali* sp. (Mimosaceae; "tangarana"), *Guarea* sp. (Meliaceae; "requia"), and few palms, mainly *Euterpe* sp. This habitat type is common on low terraces where it is subject to inundation.

### *Transect censuses*

In November and December 2012, we opened four transects of 3–5 km length at each of the four survey areas. We carried out diurnal censuses between 0630 h and 1300 h, and nocturnal censuses between 1830 h and 2200 h. Two teams of two observers each moved simultaneously along two different transects with an average speed of 1 km/h. Each transect was walked three to four times. Each time a primate group was detected the following information was recorded: group size; perpendicular distance from the transect of the first individual seen; height and activity at the moment of detection; presence of neonates and young infants; interspecific association with other primate species; and the vegetation type where the group was seen. Censuses were conducted on the transects both going out and returning. In all, we walked 610 km of transects (430 km diurnal, 180 nocturnal).

### *Data analyses*

Due to the small number of sightings (<30) for most species, we used the formula suggested by Burnham *et al.* (1980) for calculation of densities: $D = N/2dL$, where $D$ = the density (groups/km²), $N$ = the number of sightings, $L$ = the accumulated transect length, and $d$ = the mean perpendicular distance from the transect. The population density was then obtained by multiplying D by mean group size. We also calculated the number of sightings per 10 km of walked transect. We excluded *Cebuella pygmaea* from the analyses, as this species is restricted to river-edge forest, and is thus not easily recorded along transects extending away from the river.

Based on the number of sightings per species, we calculated the Euclidean distance between the primate communities of each habitat type in Ecological Methodology 7.2. To examine the similarity/dissimilarity of the communities, we subjected the resulting distance values to a single-linkage cluster analysis in Statistica 10.0.

## Results

We obtained 304 sightings of 13 primate species. Most were of *Lagothrix poeppigii* (N = 49), followed by *Callicebus discolor* (N = 32) and *Ateles belzebuth* (N = 31); the least sightings were logged for *C. pygmaea* (N = 8), and *Pithecia napensis*[1] (N = 16; Table 2). The smallest groups were those of *C. discolor*, *Aotus vociferans* and *Pithecia napensis*, and the largest were of *Saimiri macrodon* (previously *Saimiri sciureus*) and *L. poeppigii* (Table 2). The range of observed group sizes generally matched those recorded in other areas of northeastern Peruvian Amazonia, except for *A. belzebuth* which had larger groups than in other areas (Table 2).

*Saguinus tripartitus* and *P. napensis* were recorded only north of the Río Curaray, and *Saguinus lagonotus*, *P. aequatorialis* and *Sapajus macrocephalus* (previously *Cebus apella macrocephala*) only south of the Curaray (Fig. 2). The number of sightings was highest for *A. vociferans*, *L. poeppigii* and *S. lagonotus*, and the highest population densities were those of *S. macrodon* and *L. poeppigii* (Table 3).

All primate species combined, the majority of sightings were in *palmal alto* and high forest; 12 of the 13 primate species were encountered in these habitat types (Table 4). Only four and five species, respectively, were sighted in *varillal* and tree swamps (Table 4). Atelids and cebids were most frequently observed in high forest, *palmal de altura* and *palmal de planicie*. *Cebuella pygmaea* was encountered exclusively and *C. discolor* mainly in low forest. Results of the cluster analysis reflect the uneven community composition over habitat types (Fig. 3). Primate communities of *varillales* and tree swamps cluster closely together and, more distantly, with *palmales de planicie*. High forest clusters with *palmales de altura* (Fig. 3). Low forest clearly sticks out, which is due to the lack or scarcity of sightings of large and medium-sized primates (atelids, *Cebus*, and *Sapajus*) there, and the frequent sightings of small primates (callitrichids, pitheciids, and *Saimiri*).

On 30 occasions we saw two species associated with each other. Two-thirds were of squirrel monkeys *Saimiri macrodon* travelling with the capuchin monkeys *S. macrocephalus* (13 cases) or *C. yuracus* (seven cases).

## Discussion

The number of primate species encountered during our survey (13) is higher than that reported by Heymann *et al.* (2002), who did not record *A. belzebuth* and *C. pygmaea*. It matches the number of species found in the Manú National Park (Terborgh 1983) and in the Reserva Comunal Tamshiyacu-Tahuayo (now: Area de Conservación Regional Comunal

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[1] We follow the taxonomic revision of the genus *Pithecia* by Marsh (2014).

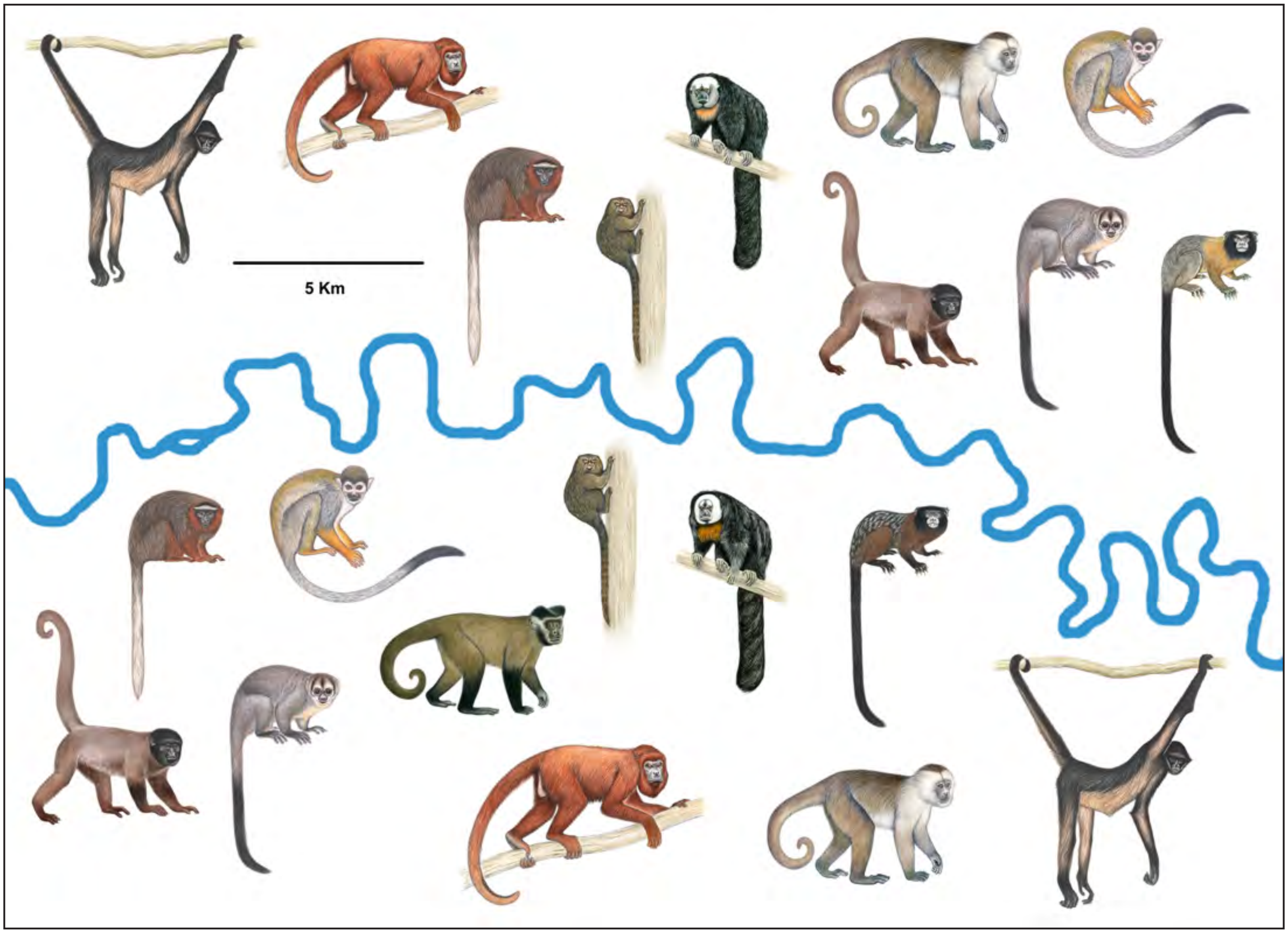

**Figure 2.** Primate communities north and south of the Rio Curaray at the four localities surveyed (see Table 1, Fig. 1). *Saguinus tripartitus* and *Pithecia napensis* were observed only north of the river (left bank), and *Saguinus lagonotus*, *Sapajus macrocephalus*, and *Pithecia aequatorialis* were observed only south of the river (right bank).

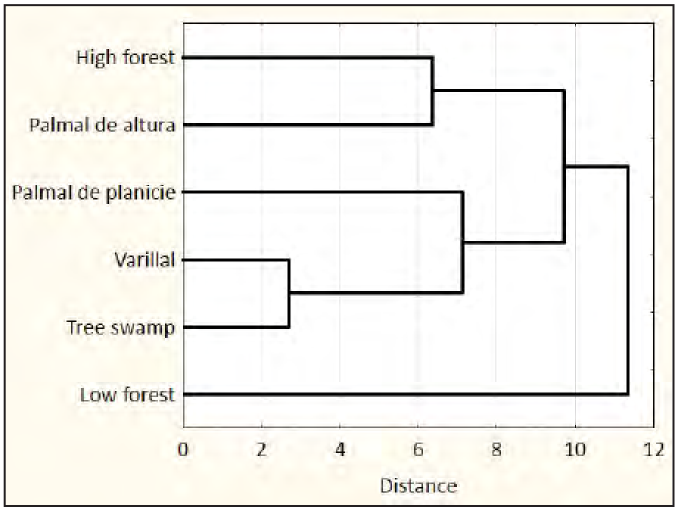

**Figure 3.** Single-linkage cluster analyses of the similarity of primate communities in the different habitat types.

Tamshiyacu-Tahuayo, ACRCTT) (Puertas and Bodmer 1993)[2]. It is higher than the number of primate species in the Yasuní National Park, Ecuador, where 10 species are found (Bass *et al.* 2010; Marsh 2004). However, not all species occur syntopically, and the maximum number of species at any survey site was 11 (on the south bank of the Curaray). This supports the prediction (Heymann *et al.* 2002) of a maximum of 10–11 species per site, and is in line with the findings of Palminteri and co-workers, who found a maximum of 10 species out of a pool of 13 at all of their survey sites in southeastern Peru (Palminteri 2010). While on a large (continental) scale, forest cover and rainfall are the major predictors of primate species richness (Peres and Janson 1999), habitat type is strongly predictive on the regional/local scale, with *terra firme* forests harboring richer primate communities than flooded forests

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2 Puertas and Bodmer (1993) reported 14 species for ACRCTT, but the presence of *Saimiri boliviensis* has not been confirmed and is actually unlikely, as the area is outside its distributional range and northeast of a known hybrid zone with *Saimiri sciureus* on the Río Ucayali (Hershkovitz 1984; Silva *et al.* 1992).

**Table 2.** Primate species and their group sizes recorded during transect censuses.

| Species* | Group size | | # of groups | | Group size range in other areas |
|---|---|---|---|---|---|
| | Mean (SD) | Range | Total | With complete counts | |
| *Ateles belzebuth* | 12.2 ± 5.5 | 6–18 | 31 | 5 | 2–11[a] |
| *Lagothrix poeppigii* | 16.0 ± 5.6 | 9–23 | 49 | 6 | 5–24[b] |
| *Alouatta seniculus* | 7.0 ± 2.4 | 6–11 | 18 | 8 | 2–13[c] |
| *Cebus yuracus* | 14.0 ± 3.2 | 9–17 | 28 | 5 | 12–16[b] |
| *Sapajus macrocephalus* | 12.2 ± 3.3 | 11–15 | 18 | 5 | 2–13[b] |
| *Pithecia aequatorialis* | 3.7 ± 1.3 | 2–6 | 19 | 9 | 2–8[b] |
| *Pithecia napensis* | 4.5 ± 2.0 | 2–7 | 16 | 6 | 2–8[c] |
| *Callicebus discolor* | 3.2 ± 1.2 | 2–5 | 32 | 13 | 2–6[b] |
| *Saimiri macrodon* | 43.5[§] | >35 | 19 | | 2–61[b] |
| *Aotus vociferans* | 3.6 ± 1.0 | 2–5 | 21 | 8 | 2–5[d] |
| *Saguinus lagonotus* | 5.8 ± 1.1 | 4–7 | 28 | 15 | 2–10[c] |
| *Saguinus tripartitus* | 5.7 ± 1.3 | 4–8 | 17 | 9 | 6–9[e] |
| *Cebuella pygmaea* | 5.6 ± 1.2 | 5–7 | 8 | 3 | 2–9[c] |

* In order of decreasing body mass
[§] Incomplete counts; therefore, mean taken from Aquino *et al.* (2009a)
Sources: [a]Río Samiria: Aquino and Bodmer (2006); [b]Río Itaya: Aquino *et al.* (2009b); [c]Pacaya Samiria: Soini (1986); [d]Río Napo: Aquino *et al.* (1990); [e]Ecuadorian Amazon: Albuja (1994)

**Table 3.** Sighting rates and population density estimates.

| Species* | Mean detection distance m | Total length of transect walks km | # of sightings/ 10 km of transect walk | Population density | | Pucacuro[a] | Itaya[b] | Arabela[c] | Yasuní[d] |
|---|---|---|---|---|---|---|---|---|---|
| | | | | groups/km² | ind./km² | ind./km² | ind./km² | ind./km² | ind./km² |
| *Ateles belzebuth* | 18 | 430[†] | 0.7 | 1.9 | 23.0 | 0.8 | - | 13.3 | 11.5 |
| *Lagothrix poeppigii* | 20 | 430[†] | 1.1 | 3.1 | 49.6 | 10.0 | 15.4 | 30.6 | 31 |
| *Alouatta seniculus* | 15 | 430[†] | 0.4 | 1.4 | 9.8 | 2.1 | 0.2 | n.a. | n.a. |
| *Cebus yuracus* | 15 | 430[†] | 0.6 | 2.1 | 29.4 | 4.4 | 6.8 | n.a. | n.a. |
| *Sapajus macrocephalus* | 14 | 230[‡] | 0.8 | 2.6 | 31.7 | 2.8 | 3.0 | n.a. | n.a. |
| *Pithecia aequatorialis* | 13 | 230[‡] | 0.8 | 3.1 | 11.5 | 2.8 | 7.8 | n.a. | n.a. |
| *Pithecia napensis* | 10 | 200[§] | 0.8 | 3.5 | 15.7 | - | - | n.a. | n.a. |
| *Callicebus discolor* | 9 | 430[†] | 0.7 | 4.3 | 13.8 | 1.1 | 7.0 | n.a. | n.a. |
| *Saimiri macrodon* | 12 | 430[†] | 0.4 | 1.4 | 61.0 | 5.2 | 18.2 | n.a. | n.a. |
| *Aotus vociferans* | 8 | 180[†] | 1.1 | 7.2 | 26.0 | n.a. | n.a. | n.a. | n.a. |
| *Saguinus lagonotus* | 10 | 230[‡] | 1.2 | 6.0 | 34.8 | 3.0 | 10.5 | 14.8 | n.a. |
| *Saguinus tripartitus* | 9 | 200[§] | 0.8 | 4.7 | 26.8 | - | - | n.a. | n.a. |

* In order of decreasing body mass; [†]all transects; [‡]transects south of the Río Curaray (1, 3); [§]transects north of the Río Curaray (2, 4); n.a. = not available
Sources: [a]Aquino *et al.* (2000a); [b] Aquino *et al.* (2009b); [c]Kolowski and Alonso (2012); [d]Dew (2005)

(Palminteri *et al.* 2011; Peres 1997). Our survey corroborates these findings, with fewer primate species in those habitats that are subject to inundation. The lowest number was found in *varillal*, which might be explained by the low floristic diversity (and probably productivity) of white-sand forests (Fine *et al.* 2010; Oñate Calvín 2012).

Our survey confirms previous observations that the Río Curaray forms a distributional limit for two species each of *Saguinus* and *Pithecia* (Aquino and Encarnación 1996; Heymann *et al.* 2002; Rylands *et al.* 2011). In line with Heymann *et al.* (2002), we encountered *S. macrocephalus* only on the south bank of the Río Curaray. However, in contrast to Heymann *et al*. (2002), we encountered *Cebus yuracus* (previously *Cebus albifrons yuracus*) on both banks. The restriction of *S. lagonotus*, *S. macrocephalus* and *P. aequatorialis* to the south bank of the Río Curaray accounts for the higher number of primate species compared to the Yasuní National Park, located north of the Río Curaray (the eastern border of which is only about 25 km from our survey area).

**Table 4.** Number of sightings of different primate species per habitat type.

| Species* | Number of sightings per habitat type | | | | | | Total |
|---|---|---|---|---|---|---|---|
| | H.f. | L.f. | P.a. | P.p. | Va | T.s. | |
| *Ateles belzebuth* | 14 | 0 | 8 | 9 | 0 | 0 | 31 |
| *Lagothrix poeppigii* | 19 | 0 | 23 | 5 | 2 | 0 | 49 |
| *Alouatta seniculus* | 2 | 0 | 6 | 7 | 0 | 3 | 18 |
| *Cebus yuracus* | 4 | 3 | 11 | 9 | 0 | 1 | 28 |
| *Sapajus apella* | 6 | 2 | 7 | 3 | 0 | 0 | 18 |
| *Pithecia aequatorialis* | 8 | 0 | 5 | 2 | 4 | 0 | 19 |
| *Pithecia napensis* | 4 | 0 | 12 | 0 | 0 | 0 | 16 |
| *Callicebus discolor* | 8 | 19 | 3 | 0 | 0 | 2 | 32 |
| *Saimiri macrodon* | 4 | 5 | 6 | 2 | 1 | 1 | 19 |
| *Aotus vociferans* | 3 | 9 | 5 | 4 | 0 | 0 | 21 |
| *Saguinus lagonotus* | 7 | 9 | 6 | 3 | 3 | 0 | 28 |
| *Saguinus tripartitus* | 4 | 7 | 5 | 0 | 0 | 1 | 17 |
| *Cebuella pygmaea* | 0 | 8 | 0 | 0 | 0 | 0 | 8 |
| Total | 83 | 62 | 97 | 44 | 10 | 8 | 304 |
| # of species / habitat | 12 | 8 | 12 | 9 | 4 | 5 | |

* in order of decreasing body mass

[#] H.f.: high forest; L.f.: low forest; P.a.: *palmal de altura*; P.p.: *palmal de planicie*; Va: *varillal*, T.s.: tree swamp

That the Río Curaray is a barrier is quite surprising, as it is quite narrow (50–100 m wide) and strongly meandering, resulting in frequent river bend cut-offs of small islands that could transfer species from one bank of the river to the other. However, as meanders of the Río Curaray are extremely constricted (see Google Earth, 1°10'S–2°30'S, 74°05'W–75°35'W), these islands may simply be too small to accommodate a population large enough to persist until merging with a population on the opposite bank of the river (Heymann *et al.* 2002).

Our population density estimates are higher than those obtained for the Río Pucacuro and the upper Río Itaya (Aquino *et al.* 2000a, 2009b). For *L. poeppigii*, *A. belzebuth* and *S. lagonotus* they are also higher than those obtained by Kolowski and Alonso (2012) in the non-hunted forest of the upper reaches of Quebrada Arabela, about 50 km from our area. Since Kolowski and Alonso (2012) used the number of individuals seen upon encounter rather than complete counts to estimate group size for calculating population densities, their estimates are inherently smaller than ours, even if real population densities were actually very similar. More importantly, the fact that both our density estimates and those of Kolowski and Alonso (2012) are consistently higher than those for the Río Pucacuro and the upper Río Itaya supports the notion that human interference affects primate population densities. This effect is particularly strong for the large atelids which are preferred by hunters (Aquino *et al.* 2000b; Peres 1990; Puertas and Bodmer 1993), but may also be pertinent for medium-sized and smaller primates (Endo *et al.* 2010). Being closer to Iquitos (where bushmeat was, and still is, common in the markets Castro *et al.* 1990), and more accessible than the upper Río Curaray, hunting pressure is much stronger at Río Pucacuro and the upper Río Itaya.

For *L. poeppigii* and *A. belzebuth* our estimates are also higher than those for the Yasuní National Park (Dew 2005). Dew obtained his estimates by relating study group size to home-range size, so again results cannot be directly compared. Nevertheless, it is noteworthy that in these two studies and in our study, the density of *L. poeppigii* was always 2–3 times higher than the density of *A. belzebuth*. While it is tempting to speculate that interspecific competition might keep population densities of *A. belzebuth* lower than those of *L. poeppigii* (Dew 2005, Iwanaga and Ferrari 2002), a reverse pattern, i.e. higher population densities for *Ateles*, has been reported from four out of five non-hunted sites in the Manú National Park (Endo *et al.* 2010). Detailed, comparative, long-term, ecological studies and biogeographic analyses are needed to reveal whether populations of *Ateles* and *Lagothrix* affect each other, whether local ecological conditions favor one or the other species, or whether historical events or processes are responsible for current patterns.

Amongst the small species (body mass <1 kg), *C. pygmaea* and *C. discolor* stick out by either having been recorded exclusively or by strongly prevailing, respectively, in a single habitat type. *Cebuella pygmaea* is a highly specialized exudativore that prefers floodplain forest (Soini 1982; de la Torre *et al.* 2000). The only available ecological study of *C. discolor* (by Carillo-Bilbao *et al.* 2005) indicates that this species uses mainly the lower canopy and the understorey, which may facilitate its existence in low forest. However, *S. tripartitus* and *S. lagonotus* also prefer the lower forest strata (Heymann 2000, Heymann *et al.* 2002), but do not prevail in low forest. Additional ecological factors must play a role that we have yet to identify. In conclusion, our survey revealed that the upper Río Curaray harbors a species-rich primate fauna, which adds to the recognition of the Río Napo region as one of the most species-rich areas of the world. To conserve this biodiversity, the creation of a protected area that includes both banks of the upper Río Curaray and that adjoins the Yasuní National Park on the Ecuadorian side would be highly desirable.

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# Revision of Madagascar's Dwarf lemurs (Cheirogaleidae: *Cheirogaleus*): Designation of Species, Candidate Species Status and Geographic Boundaries Based on Molecular and Morphological Data

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**Abstract:** The genus *Cheirogaleus*, the dwarf lemurs, is a radiation of strepsirrhine primates endemic to the island of Madagascar. The dwarf lemurs are taxonomically grouped in the family Cheirogaleidae (Infraorder: Lemuriformes) along with the genera *Microcebus, Mirza*, *Allocebus*, and *Phaner*. The taxonomic history of the genus *Cheirogaleus* has been controversial since its inception due to a paucity of evidence in support of some proposed species. In this study, we addressed this issue by expanding the geographic breadth of samples by 91 individuals and built upon existing mitochondrial (cytb and COII) and nuclear (FIBA and vWF) DNA datasets to better resolve the phylogeny of *Cheirogaleus*. The mitochondrial gene fragments D-loop and PAST as well as the CFTR-PAIRB nuclear loci were also sequenced. In agreement with previous genetic studies, numerous deep divergences were resolved in the *C. major*, *C. minor* and *C. medius* lineages. Four of these lineages were segregated as new species, seven were identified as confirmed candidate species, and four were designated as unconfirmed candidate species based on comparative mitochondrial DNA sequence data gleaned from the literature or this study. Additionally, *C. thomasi* was resurrected. Given the widespread distribution of the genus *Cheirogaleus* throughout Madagascar, the methodology employed in this study combined all available lines of evidence to standardize investigative procedures in a genus with limited access to type material and a lack of comprehensive sampling across its total distribution. Our results highlighted lineages that likely represent new species and identified localities that may harbor an as-yet undescribed cryptic species diversity pending further field and laboratory work.

**Key Words:** *Cheirogaleus*, candidate species, dwarf lemurs, Madagascar, mtDNA, nuclear DNA

## Introduction

Madagascar is an island of such proportions and unique natural history that it has been likened to a continent (de Wit 2003). The population of this biodiversity hotspot, exceeding 20 million people (INSTAT 2011), is ever-increasing its demand on forest resources to fulfill its needs, ranging from timber for construction to expanding agricultural lands (Durbin *et al.* 2003; Harper *et al.* 2007; Gorenflo *et al.* 2011). Unfortunately, an estimated 90% of Madagascar's endemic wildlife resides in these overtaxed forest ecosystems (Dufils 2003). The result of this is a crisis of survival for the most threatened large group of mammals on Earth, the lemurs (Schwitzer *et al.* 2014). Often referred to as the country's flagship species-group, additional research is required to properly characterize the diversity of these strepsirrhine primates.

The identification of new lineages is vital to the preservation of biodiversity. Bringing to light previously unknown species allows for more informed decisions regarding conservation funding and the designation of protected areas (DeSalle and Amato 2004). Advancements in molecular technology, combined with improvements in analytical tools and intensive field investigation, have greatly increased the number of described lemur species in less than three decades—from 36 in 1982 (Tattersall 1982) to more than 100 today (Thalmann 2007; Tattersall 2007, 2013; Mittermeier *et al.* 2008, 2010; Lei *et al.* 2012; Thiele *et al.* 2013). This taxonomic explosion has been especially notable in the family Cheirogaleidae, where the number of recognized species in the genus *Microcebus* increased from two (Tattersall 1982) to 21 based on the evaluation of mitochondrial DNA (mtDNA) sequence fragments and morphological data (Schmid and Kappeler 1994; Zimmermann *et al.* 1998; Rasoloarison *et al.* 2000, 2013; Kappeler *et al.* 2005; Andriantompohavana *et al.* 2006; Louis *et al.* 2006, 2008; Olivieri *et al.* 2007; Radespiel *et al.* 2008, 2012). Such work has not involved detailed field study of interfertility, and instead relied largely on biogeographic inference, molecular data, and the Phylogenetic Species Concept (PSC; Eldredge and Cracraft 1980; Wheeler and Platnick 2000).

Although the genus *Cheirogaleus*, the dwarf lemurs, is closely related and ecologically similar to *Microcebus*, a comparable radiation has yet to be confirmed. The broadest circumscription of *Cheirogaleus* included seven species (Groves 2000), with more than a century lapsing between the identification of new species (Forsyth Major 1896). This comparatively low diversity may be more of an artifact of incomplete sampling than a reflection of the true state of dwarf lemur diversity, as indicated by recent genetic investigations (Hapke *et al.* 2005; Groeneveld *et al.* 2009, 2010; Thiele *et al.* 2013). An effective exploration of the evolution of *Cheirogaleus* with broader genetic sampling is warranted, but should be conducted with regard to historical specimens and literature to ensure the careful application of names to identified lineages. However, gaining a historical perspective on this genus has proved complicated (Groves 2000).

The circumscription of *Cheirogaleus* was suspect right from its inception. The first species were provisionally described by É. Geoffroy St. Hilaire (1812) based on drawings by Commerçon, which he thought to be faithful representations of lemurs seen in the field. Later study of these three illustrations indicated that they were drawn not directly from specimens, but from memory. This was evidenced by the fact that they had features uncharacteristic of this group, such as claws (Groves 2000). Thus, the initial species concepts were flawed, and the genus was vulnerable to synonymization, resurrection, lumping, splitting, and rearrangements (Wolf 1822; Smith 1833; Lesson 1840; Gray 1872; Forsyth Major 1894, 1896; Elliot 1913; Schwarz 1931; Groves 2000).

Some of the discord in *Cheirogaleus* taxonomic systems, the majority of which were published before 1900, stemmed from the paltry number of specimens available for study. A review of historical documents and museum collection databases showed that prior to the turn of the 20th century there were only about 50 specimens, many incomplete, deposited in a handful of European institutions: the Natural History Museum, London (formerly British Museum (Natural History) BMNH), Muséum National d'Histoire Naturelle (MNHN), Museum für Naturkunde Berlin (MfN, also known as ZMB), and Naturalis Biodiversity Center, formerly Rijksmuseum van Naturlijk Historie (NMNL). Although these specimens were invaluable for introducing dwarf lemurs to the world outside Madagascar, they were insufficient to accurately delimit species based on morphology and anatomy, and these difficulties were compounded by vague collection localities. Schwarz (1931) recognized these challenges and acknowledged that his narrow classification of *Cheirogaleus* was the weakest in his revision of Madagascar's lemurs.

Groves (2000), referring to Schwarz's (1931) work as oversimplified, mounted an extensive morphological study on the same museum specimens as well as on more recent additions. He designated neotypes for *C. major* and *C. medius* in order to fix the names so that other species could be recognized. Unfortunately, there is no type locality information for the *C. major* neotype, but the type locality for *C. medius* is along the Tsiribihina River, previously known as the Tsidsibon River (Goodman and Rakotondravony 1996), in western Madagascar. In addition to the two aforementioned species, Groves also accepted *C. crossleyi*, *C. adipicaudatus*, *C. sibreei*, *C. ravus*, and *C. minusculus*. The species circumscriptions from this work were valuable in laying the foundation for the genetic studies that were to follow.

Using mitochondrial Cytochrome b (cytb) sequences to investigate three morphotypes near Tolagnaro in southeastern Madagascar, Hapke *et al.* (2005) confirmed the existence of three distinct lineages corresponding to Groves's (2000) accepted species. These monophyletic clades were identified as *C. major*, *C. medius*, and *C. crossleyi* based on genetic and morphological comparisons with museum specimens (Hapke *et al.* 2005). The authors did note extensive intraspecific genetic distances, in some cases greater than that found between species of mouse lemurs, within the latter two clades. Further study was encouraged, in particular into the putative southern *C. crossleyi* population and a notable population of *C. medius* in Ankarana in northern Madagascar (Hapke *et al.* 2005).

The existence of strong mitochondrial phylogeographic structure hinted at by Hapke *et al.* (2005) within the *C. medius*, *C. major* and *C. crossleyi* groups was confirmed using an expanded dataset by Groeneveld *et al.* (2009, 2010). This was echoed by Thiele *et al.* (2013) who stressed the existence of unnamed diversity contained within these highly variable units based on the same mtDNA and nuclear sequence data. This resulted in the description of a new species, *C. lavasoensis*, corresponding to Hapke *et al.*'s (2005) divergent southern *C. crossleyi* lineage. Three other species were also proposed, but not described, and were provisionally referred to as *Cheirogaleus* sp. Ranomafana Andrambovato, *C.* sp. Bekaraoka Sambava, and *C.* sp. Ambanja (Thiele *et al.* 2013).

Although many of the species accepted by Groves have been supported, *C. adipicaudatus* and *C. ravus* were synonymized with *C. medius* and *C. major*, respectively, in genetic studies that combined historical and contemporary specimens (Groeneveld *et al.* 2009, 2010). Thus, there are currently six accepted species: *C. major*, *C. medius*, *C. crossleyi*, *C. lavasoensis*, *C. sibreei*, and *C. minusculus*. *C. minusculus* and *C. major* are considered Data Deficient according to IUCN's Red List, while the widespread and morphologically variable *C. medius* is listed as Least Concern (Andrainarivo *et al.* 2013). *C. sibreei* is listed as Critically Endangered, and *C. lavasoensis* is in a similarly dire situation, having been provisionally named to the upcoming list of the World's 25 Most Endangered Primates 2014–2016 (R. A. Mittermeier, unpubl.). The possibility of segregating additional cryptic taxa from *C. medius* and *C. major* would result in narrower ranges for these species, and the entire genus would be in need of reassessment.

As Groves (2000) designated neotypes for *C. major* and *C. medius*, this work intends to provisionally link those names to their corresponding clades as well as to that of *C. crossleyi*. Once accomplished, clades that represent lineages distinct from those already named can be assessed. To accomplish this, in this study a general work protocol (proposed by Padial *et al.* 2010) was applied that integrates all available evidence in taxonomic practice to standardize the species delimitation process according to the Phylogenetic Species Concept (PSC; Eldredge and Cracraft 1980; Wheeler and Platnick 2000). The number and geographic breadth of *Cheirogaleus* specimens was increased by 91 individuals from throughout the genus' range and the mtDNA and nuclear sequence data sets were enlarged. Geographic regions harboring potential new species were identified and put into context with historical type specimens and localities.

## Methods

### *Sampling collection*

From 1999 to 2008, 91 *Cheirogaleus* samples were collected from 31 different localities throughout Madagascar (Table 1; Fig. 1; Appendix II(a)). Of the currently accepted species, only *C. minusculus* could not be assessed as comparable field samples from the Ambositra area could not be obtained for this study. The lemurs were immobilized with a $CO_2$ projection rifle or blowgun as described in Louis *et al.* (2006). Whole blood (1.0 cc/kg) and four 2 mm biopsies were collected and placed in room temperature preservative (Seutin *et al.* 1991) until transferred to the laboratory for storage at -80 °C. All collection and export permits were obtained from the Ministère de l'Environnement, de l'Ecologie et des Forêts and samples were imported to the United States with appropriate Convention for International Trade in Endangered Species (CITES) permits. We recorded the GPS coordinates to accurately identify the capture location of each animal so that it could be released where it was initially caught (Table 1). Morphometric measurements were taken on sedated animals as described in Louis *et al.* (2006) and Andriantompohavana *et al.* (2007). Museum samples listed in Appendices IIb-IId were measured as in Groves (2000).

### *Data generation*

Genomic DNA was extracted from samples using a phenol-chloroform extraction method (Sambrook *et al.* 1989). To correlate our data with previously published molecular studies, we analyzed the following regions of the mtDNA: Cytochrome b (cytb) (Irwin *et al.* 1991); Cytochrome oxidase subunit II (COII) (Adkins and Honeycutt 1994); the displacement loop or control region (D-loop) (Baker *et al.* 1993; Wyner *et al.* 1999); a fragment of the Cytochrome oxidase subunit III gene (COIII); NADH-dehydrogenase subunits 3, 4L, and 4 (ND3, ND4L, and ND4); as well as the $tRNA^{Gly}$, $tRNA^{Arg}$, $tRNA^{His}$, $tRNA^{Ser}$, and partial $tRNA^{Leu}$ genes (PAST) (Pastorini *et al.* 2000). Three independent nuclear loci were also amplified: alpha fibrinogen intron 4 (FIBA), von Willebrand Factor intron 11 (vWF) and Cystic Fibrosis Transmembrane conductance (CFTR-PAIRB), which were the same loci used in Heckman *et al.* (2007) and Horvath *et al.* (2008). The thermocycler profile conditions were as follows: 95°C for 2 min; 34 cycles of 94°C for 30 sec, 45°C–60°C (Appendix II(e)) for 45 sec, 72°C for 45 sec; 72°C for 10 min. PCR amplifications were carried out in 25 µl reaction volumes containing 2–5 ng of total genomic DNA, 12.5 µM of each primer, 200 µM dNTPs, 10 mM Tris-HCl, 1.5 mM $MgCl_2$, 100 mM KCl (pH 8.0) and 0.5 units of BIOLASE™ Taq DNA Polymerase (Bioline USA Inc., Randolph, MA).

PCR products were confirmed, purified, and sequenced as in Lei *et al.* (2012). Additionally, PCR and sequencing primers specific for *Cheirogaleus* were designed for the cytb, COII, D-loop, PAST fragment, FIBA, vWF, and CFTR-PAIR (Appendix II(e)). Accessioned sequences were used to compare and augment the datasets to evaluate the current taxonomic knowledge of the genus *Cheirogaleus* (Hapke *et al.* 2005; Groeneveld *et al.* 2009, 2010; Thiele *et al.* 2013; see Appendix II(f)).

### *Phylogenetic analysis*

The sequences were edited and aligned using Sequencher v4.10 (Gene Corp, Ann Arbor, Michigan). All sequences (accession numbers KM872106-KM872736) have been deposited in GenBank. MEGA v4.0 (Tamura *et al.* 2007) was used to calculate parsimony informative sites and uncorrected "p" distances for cytb, COII, D-loop, PAST fragments and three nuclear marker sequences. Based on the sequence divergence criteria of Thiele *et al.* (2013), we subdivided *C. crossleyi* into groups Crossleyi A–E, *C. major* into groups Major A–C, *C. medius* into groups Medius A–H and *C. sibreei* formed one group Csi. All genetic data were used for subsequent maximum likelihood (ML) and Bayesian phylogenetic analyses. Optimal nucleotide substitution models for each locus were chosen using the Akaike Information Criterion (AIC) as implemented in Modeltest v3.7 (Posada and Crandall 1998). All ML analyses were performed using a genetic algorithm approach in Garli v0.951 (Zwickl 2006) under the models specified by the AIC in Modeltest. Twenty-five replicates were run for each data set to verify consistency in log likelihood (ln L) scores and tree topologies. Maximum likelihood bootstrap percentages (BP) were estimated in Garli by performing 200 pseudoreplicates on all data sets. PAUP* 4.0b10 (Swofford 2001) was then used to calculate a majority-rule consensus tree for each data set and to visualize the phylogenetic trees.

Bayesian inference analyses of each data set were conducted using MrBayes v3.1.2 (Huelsenbeck *et al.* 2001; Ronquist and Huelsenbeck 2003). The model of evolution was

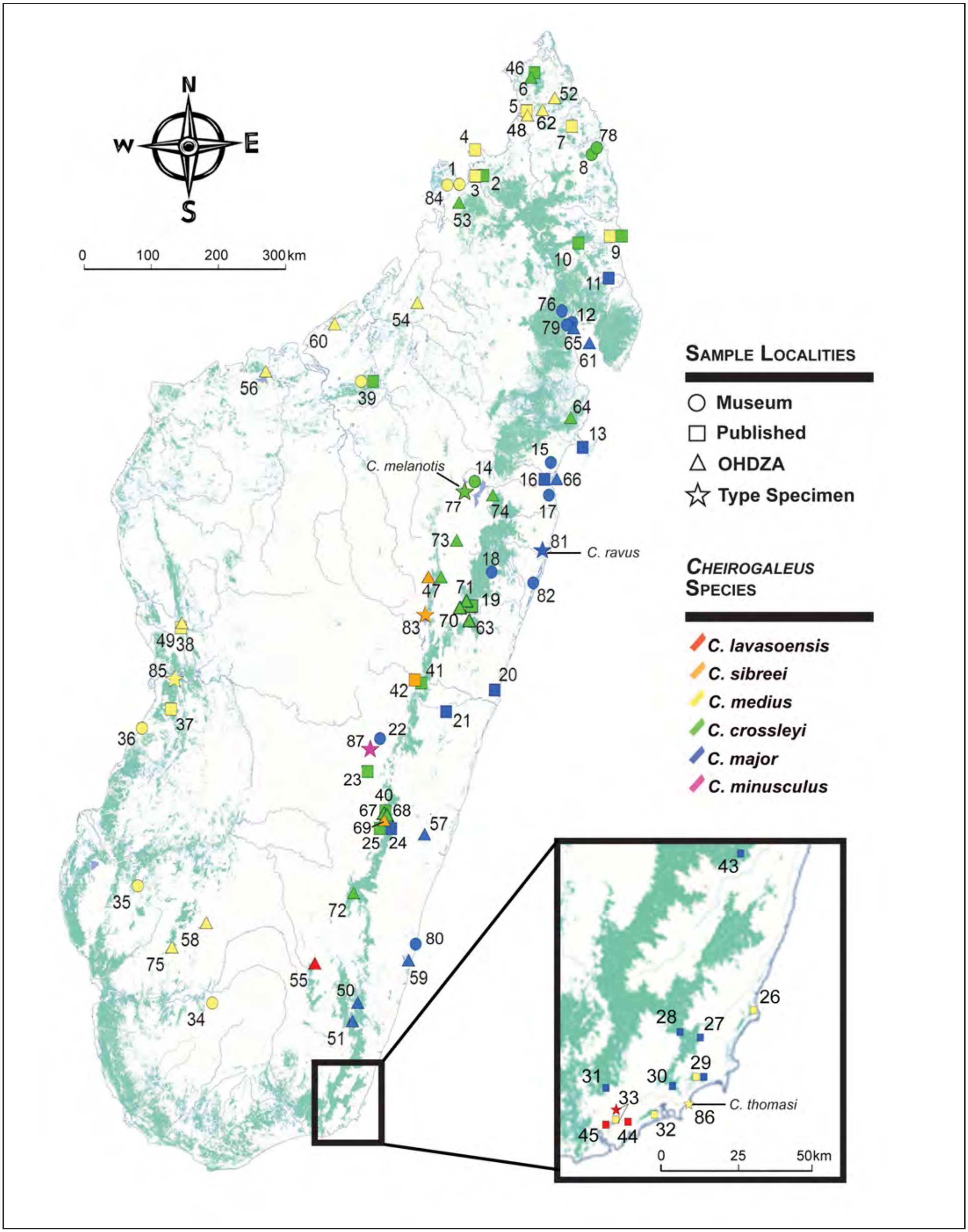


**Figure 1.** Map of sampling localities of the dwarf lemurs of Madagascar. Triangles represent sites sampled for this study; squares denote sampling localities of recently published field samples; circles represent presumed georeferenced sampling localities of museum specimens. Detailed information for locality sites, marked by locality number, is shown in Table 1 and Appendices II(a,d).

**Table 1.** Free-ranging *Cheirogaleus* samples used in this study.

| ID | Original species designation | Current species designation | Location | Locality number | Latitude | Longitude | Clade |
|---|---|---|---|---|---|---|---|
| AMB5.22 | *C. crossleyi* | CCS1 | Montagne d'Ambre | 46 | -12.52731 | 49.17331 | Crossleyi A |
| AMB5.23 | *C. crossleyi* | CCS1 | Montagne d'Ambre | 46 | -12.53017 | 49.17464 | Crossleyi A |
| AMB5.27 | *C. crossleyi* | CCS1 | Montagne d'Ambre | 46 | -12.51722 | 49.17950 | Crossleyi A |
| AMB5.28 | *C. crossleyi* | CCS1 | Montagne d'Ambre | 46 | -12.47881 | 49.21222 | Crossleyi A |
| AMB5.29 | *C. crossleyi* | CCS1 | Montagne d'Ambre | 46 | -12.47922 | 49.21606 | Crossleyi A |
| AMB5.30 | *C. crossleyi* | CCS1 | Montagne d'Ambre | 46 | -12.47917 | 49.21597 | Crossleyi A |
| AMB5.31 | *C. crossleyi* | CCS1 | Montagne d'Ambre | 46 | -12.51083 | 49.19275 | Crossleyi A |
| AMB5.32 | *C. crossleyi* | CCS1 | Montagne d'Ambre | 46 | -12.51242 | 49.18956 | Crossleyi A |
| AMB5.34 | *C. crossleyi* | CCS1 | Montagne d'Ambre | 46 | -12.47822 | 49.21717 | Crossleyi A |
| AMB5.35 | *C. crossleyi* | CCS1 | Montagne d'Ambre | 46 | -12.49519 | 49.20783 | Crossleyi A |
| ANJZ1 | *C. crossleyi* | *C. crossleyi* | Anjozorobe | 47 | -18.47750 | 47.93812 | Crossleyi B |
| ANJZ2 | *C. crossleyi* | *C. crossleyi* | Anjozorobe | 47 | -18.47750 | 47.93812 | Crossleyi B |
| ANJZ3 | *C. crossleyi* | *C. crossleyi* | Anjozorobe | 47 | -18.47750 | 47.93812 | Crossleyi B |
| ANK5.12 | *C. medius* | CCS6 | Ankarana | 48 | -12.96631 | 49.13808 | Medius A |
| ANK5.13 | *C. medius* | CCS6 | Ankarana | 48 | -12.96631 | 49.13808 | Medius A |
| ANK5.14 | *C. medius* | CCS6 | Ankarana | 48 | -12.96631 | 49.13808 | Medius A |
| ANK5.15 | *C. medius* | CCS6 | Ankarana | 48 | -12.96631 | 49.13808 | Medius A |
| ANK5.16 | *C. medius* | CCS6 | Ankarana | 48 | -12.96631 | 49.13808 | Medius A |
| ANK5.17 | *C. medius* | CCS6 | Ankarana | 48 | -12.96631 | 49.13808 | Medius A |
| ANK5.18 | *C. medius* | CCS6 | Ankarana | 48 | -12.96631 | 49.13808 | Medius A |
| ANK5.19 | *C. medius* | CCS6 | Ankarana | 48 | -12.96631 | 49.13808 | Medius A |
| ANK5.20 | *C. medius* | CCS6 | Ankarana | 48 | -12.96631 | 49.13808 | Medius A |
| ANK5.21 | *C. medius* | CCS6 | Ankarana | 48 | -12.96631 | 49.13808 | Medius A |
| BEMA7.19 | *C. medius* | *C. medius* | Tsingy de Bemaraha | 49 | -19.04525 | 44.77772 | Medius B |
| BEMA7.21 | *C. medius* | *C. medius* | Tsingy de Bemaraha | 49 | -19.04581 | 44.78119 | Medius B |
| BEMA7.22 | *C. medius* | *C. medius* | Tsingy de Bemaraha | 49 | -19.05383 | 44.78075 | Medius B |
| DOG14 | *C. major* | CCS4 | Midongy du Sud | 50 | -23.52111 | 47.08803 | Major A |
| DOG8.2 | *C. major* | CCS4 | Beharena Sagnira Midongy | 50 | -23.52464 | 47.09236 | Major A |
| DOG8.3 | *C. major* | CCS4 | Beharena Sagnira Midongy | 50 | -23.52161 | 47.08717 | Major A |
| DOG8.4 | *C. major* | CCS4 | Beharena Sagnira Midongy | 50 | -23.52064 | 47.09025 | Major A |
| DONGY8.4 | *C. major* | CCS4 | Ampasy Midongy | 51 | -23.74075 | 47.02592 | Major A |
| DONGY8.5 | *C. major* | CCS4 | Ampasy Midongy | 51 | -23.74272 | 47.03344 | Major A |
| DONGY8.6 | *C. major* | CCS4 | Ampasy Midongy | 51 | -23.74458 | 47.02656 | Major A |
| FIA5.19 | *C. medius* | CCS6 | Andrafiamena (Anjakely) | 52 | -12.91539 | 49.31956 | Medius A |
| FIA5.22 | *C. medius* | CCS6 | Andrafiamena (Anjakely) | 52 | -12.91539 | 49.31956 | Medius A |
| GAR8 | *C. crossleyi* | CCS2 | Manongarivo | 53 | -14.02369 | 48.27233 | Crossleyi C |
| HIH7.3 | *C. medius* | UCS2 | Anjiamangirana | 54 | -15.21642 | 47.75189 | Medius D |
| HIH9 | *C. medius* | UCS2 | Anjiamangirana (Antsohihy) | 54 | -15.15692 | 47.73311 | Medius D |
| JOZO4.7 | *C. crossleyi* | *C. crossleyi* | Anjozorobe | 47 | -18.46789 | 47.94131 | Crossleyi B |
| JOZO4.8 | *C. crossleyi* | *C. crossleyi* | Anjozorobe | 47 | -18.46789 | 47.94131 | Crossleyi B |
| JOZO4.9 | *C. crossleyi* | *C. crossleyi* | Anjozorobe | 47 | -18.46789 | 47.94131 | Crossleyi B |
| JOZO4.10 | *C. crossleyi* | *C. crossleyi* | Anjozorobe | 47 | -18.46789 | 47.94131 | Crossleyi B |
| JOZO4.17 | *C. sibreei* | *C. sibreei* | Anjozorobe | 47 | -18.46789 | 47.94131 | *C. sibreei* |
| KAL7.7 | *C. crossleyi* | *C. lavasoensis* | Kalambatritra (Sahalava) | 55 | -23.53672 | 46.53350 | Crossleyi E |
| KIBO7.9 | *C. medius* | UCS1 | Tsiombikibo | 56 | -16.04886 | 45.81067 | Medius C |
| LAKI5.18 | *C. major* | CCS5 | Lakia | 57 | -21.51558 | 47.91147 | Major B |
| LAKI5.19 | *C. major* | CCS5 | Lakia | 57 | -21.51558 | 47.91147 | Major B |
| LAKI5.26 | *C. major* | CCS5 | Lakia | 57 | -21.51558 | 47.91147 | Major B |
| LAVA1 | *C. medius* | *C. medius* | Analalava | 58 | -22.59242 | 45.13333 | Medius B |
| LAVA45 | *C. medius* | *C. medius* | Analalava | 58 | -22.58778 | 45.12803 | Medius B |
| MAB4.9 | *C. major* | CCS4 | Manombo | 59 | -23.01228 | 47.73281 | Major A |
| MAR30 | *C. medius* | UCS3 | Mariarano | 60 | -15.47992 | 46.69333 | Medius E |
| MAS6.10 | *C. major* | *C. major* | Masoala (Masiaposa) | 61 | -15.67189 | 49.96617 | Major C |
| MAS6.8 | *C. major* | *C. major* | Masoala (Masiaposa) | 61 | -15.67122 | 49.96375 | Major C |
| MAS6.9 | *C. major* | *C. major* | Masoala (Masiaposa) | 61 | -15.67150 | 49.96417 | Major C |
| MATY5.31 | *C. medius* | CCS6 | Analamera (Ampasimaty) | 62 | -12.76556 | 49.48358 | Medius A |
| MATY5.40 | *C. medius* | CCS6 | Analamera (Ampasimaty) | 62 | -12.76703 | 49.48358 | Medius A |
| MATY5.42 | *C. medius* | CCS6 | Analamera (Ampasimaty) | 62 | -12.77136 | 49.48303 | Medius A |

**Table 1.** continued

| ID | Original species designation | Current species designation | Location | Locality number | Latitude | Longitude | Clade |
|---|---|---|---|---|---|---|---|
| MIZA16 | *C. crossleyi* | *C. crossleyi* | Maromizaha | 63 | -18.97375 | 48.46461 | Crossleyi B |
| MIZA19 | *C. crossleyi* | *C. crossleyi* | Maromizaha | 63 | -18.97067 | 48.46431 | Crossleyi B |
| MIZA6.1 | *C. crossleyi* | *C. crossleyi* | Maromizaha | 63 | -18.95694 | 48.49236 | Crossleyi B |
| MIZA6.2 | *C. crossleyi* | *C. crossleyi* | Maromizaha | 63 | -18.95694 | 48.49236 | Crossleyi B |
| MIZA7.1 | *C. crossleyi* | *C. crossleyi* | Maromizaha | 63 | -18.95694 | 48.49236 | Crossleyi B |
| NARA8.2 | *C. major* | *C. major* | Mananara-Nord (Ambavala) | 64 | -16.55831 | 49.73422 | Major C |
| NOSY46 | *C. major* | *C. major* | Nosy Mangabe | 65 | -15.49539 | 49.76256 | Major C |
| POLO5.2 | *C. major* | *C. major* | Tampolo | 66 | -17.28989 | 49.40753 | Major C |
| POLO5.20 | *C. major* | *C. major* | Tampolo | 66 | -17.28747 | 49.40858 | Major C |
| POLO5.21 | *C. major* | *C. major* | Tampolo | 66 | -17.28783 | 49.40894 | Major C |
| RANO229 | *C. crossleyi* | CCS3 | Ranomafana (Talatakely) | 67 | -21.24833 | 47.42406 | Crossleyi D |
| RANO2.95 | *C. crossleyi* | CCS3 | Ranomafana (Vatoharanana) | 68 | -21.29250 | 47.43842 | Crossleyi D |
| RIR01 | *C. sibreei* | *C. sibreei* | Maharira | 69 | -21.32367 | 47.40786 | *C. sibreei* |
| TAD4.10 | *C. crossleyi* | *C. crossleyi* | Mantadia | 70 | -18.80942 | 48.42731 | Crossleyi B |
| TAD4.11 | *C. crossleyi* | *C. crossleyi* | Mantadia | 70 | -18.80942 | 48.42731 | Crossleyi B |
| TAD4.12 | *C. crossleyi* | *C. crossleyi* | Mantadia | 70 | -18.80942 | 48.42731 | Crossleyi B |
| TOR6.2 | *C. crossleyi* | *C. crossleyi* | Torotorofotsy | 71 | -18.83658 | 48.34719 | Crossleyi B |
| TORO8.11 | *C. crossleyi* | *C. crossleyi* | Torotorofotsy | 71 | -18.77044 | 48.42814 | Crossleyi B |
| TORO8.16 | *C. crossleyi* | *C. crossleyi* | Torotorofotsy | 71 | -18.76856 | 48.42475 | Crossleyi B |
| TRA8.81 | *C. crossleyi* | CCS3 | Andringitra (Ambarongy) | 72 | -22.22269 | 47.01889 | Crossleyi D |
| TRA8.82 | *C. crossleyi* | CCS3 | Andringitra (Ambarongy) | 72 | -22.22292 | 47.01950 | Crossleyi D |
| TVY7.12 | *C. crossleyi* | *C. crossleyi* | Ambatovy | 73 | -18.85086 | 48.29256 | Crossleyi B |
| TVY7.196B | *C. crossleyi* | *C. crossleyi* | Ambatovy | 73 | -18.86433 | 48.31136 | Crossleyi B |
| TVY7.197 | *C. crossleyi* | *C. crossleyi* | Ambatovy | 73 | -18.86658 | 48.30972 | Crossleyi B |
| TVY7.199 | *C. crossleyi* | *C. crossleyi* | Ambatovy | 73 | -18.87294 | 48.30500 | Crossleyi B |
| TVY7.20 | *C. crossleyi* | *C. crossleyi* | Ambatovy | 73 | -18.84797 | 48.29433 | Crossleyi B |
| TVY7.200 | *C. crossleyi* | *C. crossleyi* | Ambatovy | 73 | -18.86883 | 48.30975 | Crossleyi B |
| TVY7.206 | *C. crossleyi* | *C. crossleyi* | Ambatovy | 73 | -18.87289 | 48.30453 | Crossleyi B |
| TVY7.207 | *C. crossleyi* | *C. crossleyi* | Ambatovy | 73 | -18.87178 | 48.30297 | Crossleyi B |
| TVY7.22 | *C. crossleyi* | *C. crossleyi* | Ambatovy | 73 | -18.85017 | 48.29200 | Crossleyi B |
| TVY7.33 | *C. crossleyi* | *C. crossleyi* | Ambatovy | 73 | -18.85086 | 48.29256 | Crossleyi B |
| ZAH240 | *C. crossleyi* | *C. crossleyi* | Zahamena | 74 | -17.48917 | 48.74722 | Crossleyi B |
| ZOM6.2 | *C. medius* | *C. medius* | Zombitse | 75 | -22.88631 | 44.69375 | Medius B |

selected by using MrModeltest v2.2 (Nylander 2004). Two simultaneous Markov Chain Monte Carlo (MCMC) runs with four chains each at the default temperature were performed for 5,000,000 generations. Majority-rule consensus trees were constructed from 50,000 sample trees in PAUP* 4.0b10 for each data set (Swofford 2001). Topologies prior to –ln likelihood of equilibrium were discarded as burnin, and clade posterior probabilities (PP) were computed from the remaining trees.

We implemented the coalescent-based Bayesian species tree inference method using the software *BEAST (Drummond and Rambaut 2007; Heled and Drummond 2010) (an extension of BEAST v1.8.0). This software also implements a Bayesian MCMC analysis, and is able to co-estimate species trees and gene trees simultaneously. "Species tree" was used in the sense of Heled and Drummond (2010) here and in the following to distinguish this method from other analyses of combined data. For comparison to Thiele *et al*. (2013), we randomly selected one individual from each *Cheirogaleus* lineage to create two datasets: nuclear and a combined nuclear and mtDNA data set. Monophyly constraints were applied to the *Cheirogaleus* ingroups. The split between *Cheirogaleus* and *Microcebus* was used as a calibration point for divergence time estimates with a normal prior (mean = 23.0 Ma, Standard deviation = 2.4 Ma) on the divergence time of the root node to the species trees in all analyses, which was based on Horvath *et al.* (2008) and Thiele *et al.* (2013). Analyses were performed based on each locus in the *Cheirogaleus* dataset. Separate substitution models for each locus were utilized (HDZ dataset: GTR+G, COII: GTR+I+G, cytb: HKY+I+G, DLP: GTR+I+G, PAST: HKY, CFTR: HKY+G, FIBA: HKY + G, vWF: HKY + G; Combined dataset: GTR+I+G, cytb: HKY+G, FIBA: HKY+G, vWF). The input file was formatted with the BEAUti utility included in the software package, using the same partition scheme of the concatenated analysis.

Although *BEAST does not require the inclusion of outgroups for rooting purposes, *Microcebus ravelobensis* was incorporated in the analysis. The *BEAST analysis was conducted using a relaxed uncorrelated lognormal clock model, a random starting tree, and a speciation Yule process as the tree prior. Each run comprised 100,000,000 generations sampled every 10,000th generation. The post-burnin samples from the two independent runs were combined with a burnin of 10% for both datasets. Convergence of the MCMC was assessed by examining trace plots and histograms in Tracer v1.6 after obtaining an effective sample size (ESS) greater than 200 for all model parameters (Rambaut and Drummond 2009). A maximum clade credibility tree was generated using the program TreeAnnotator v1.8.0 provided in the BEAST package, with a burnin of 1000 (10%) and visualized in FigTree v1.3.1 (Drummond and Rambaut 2007; Rambaut 2009).

As described in Davis and Nixon (1992) and Louis *et al.* (2006), we used MacClade 3.01 (Maddison and Maddison 1992) and MEGA v4.0 (Tamura *et al.* 2007) in a diagnostic search to designate evolutionarily significant units (ESU) for the *Cheirogaleus* species using a population aggregate analysis (PAA) of the sequence data. With the sequential addition of each individual without an *a priori* species designation, a PAA distinguishes attributes or apomorphic characters according to the smallest definable unit (Davis and Nixon 1992; Louis *et al.* 2006).

To further corroborate the validity of each ESU, we implemented a system to categorize and assemble all lines of evidence from the available ecological and genetic data. Thus, deep genealogical lineages of *Cheirogaleus* were classified based on framework by Vieites *et al.* (2009), Padial *et al.* (2010) and Ratsoavina *et al.* (2013). First, the currently valid species names were assigned to lineages based on diagnostic morphological characters, taxonomy, and assignment of sequences from populations close to or at type localities when known. Second, based on the amount of evidence available from other data sets, unnamed lineages were classified as confirmed candidate species (CCS) or unconfirmed candidate species (UCS). The lineages referred to as CCS are strongly supported by morphological, genetic, and biogeographic evidence and most likely represent distinct species that were not previously scientifically named. The lineages that were denoted as UCS require additional evidence, thus the taxonomic status remains unclear.

## Results

### *Sequence data*

A concatenated mtDNA dataset with cytb, D-loop and PAST fragments was assembled only with data from the 91 field samples collected for this study (Fig. 1, Table 1) as the sequence information on all of these fragments was not available for samples used in previous studies. This yielded 4,826 bp of aligned data that contained 1,550 variable sites and 1,440 parsimony informative sites (Table 2). The complete cytb sequences of this study were aligned with the 124 *Cheirogaleus* cytb accessioned sequences from GenBank, which resulted in a total set of 98 haplotypes defined through 384 variable sites. The 48 *Cheirogaleus* COII published sequences from GenBank were aligned with sequences from this study resulting in 191 variable sites defining 55 haplotypes.

The concatenated nucDNA datasets from 91 field samples amounted to 2,337 bp, which contained 163 variable sites and 120 parsimony informative sites (Table 2). There were four bp insertions at site 377–380 (TGAT) in the CFTR-PAIRB fragment of *C. sibreei*. In the vWF alignment, there were two individuals carrying alleles with a deletion of 242 bp from the Medius B clade which were collected in Zombitse and Analalava. Combining the FIBA and vWF published sequences from GenBank and sequences of this study resulted in a data set of 208 sequences. There were 45 variable sites among 606 bp of FIBA fragment sequences. The 795 bp vWF fragment had 108 variable sites. In addition, there were 11 individuals carrying alleles with a deletion of 242 bp, all of which are from either Medius B or Medius G (Groeneveld *et al.* 2010). There are 21 individuals carrying alleles with a deletion of 19 bp, all of which were from Medius A and F distributed in northern Madagascar except for one sample from Tsingy de Bemaraha (Medius B) (Groeneveld *et al.* 2010). There were three bp deletions at sites 200–202 (CAT) and two bp insertions at sites 610–611 (AG) in the vWF fragment of *C. sibreei*.

The three mitochondrial data sets best fit a GTR+I+G model according to AIC for both ML and Bayesian analyses except the D-loop, cytb, COII and PAST data sets with TVM+I+G for ML analyses (Table 2). The vWF locus was found to best fit an HKY+I+G model for both ML and Bayesian analyses, while the CFTR-PAIRB+FIBA+vWF data set best fit a GTR+I+G model for both ML and Bayesian analyses. A TVM+I+G model was favored for the FIBA locus (analyzed under a GTR+I+G model in Bayesian phylogenetic analyses).

### *Genetic distances*

The uncorrected p-distances of the four mtDNA and three nucDNA sequence alignments were presented in Appendices II(g–m). In mtDNA sequence alignments, distances between 18 *Cheirogaleus* clades ranged from 0.021 to 0.142 in cytb (Appendix II(g)), from 0.021 to 0.149 in PAST (Appendix II(h)), from 0.045 to 0.224 in D-loop (Appendix II(i)) and from 0.016 to 0.126 in COII (Appendix II(j)). Distances between the five most closely related clades ranged from 0.021 to 0.042 in cytb, from 0.021 to 0.044 in PAST, from 0.038 to 0.054 in D-loop and from 0.016 to 0.035 in COII. The greatest intra-clade distances were 0.014 in cytb, 0.011 in PAST, 0.029 in D-loop, and 0.019 in COII. Based on genetic distance, we subdivided *Cheirogaleus crossleyi* into clades Crossleyi A–E; *C. medius* into Medius A–H; and *C. major* into Major A–C. *Cheirogaleus sibreei* formed one group (Table 1).

In nucDNA sequence alignments, distances between 18 *Cheirogaleus* clades ranged from 0.000 to 0.011 in CFTR-PAIRB (Appendix II(k)), from 0.000 to 0.007 in FIBA (Appendix II(l)) and from 0.000 to 0.016 in vWF (Appendix II(m)). The distances between clades of *C. crossleyi* were negligible, as were the distances between clades of *C. major* and *C. medius*.

### *Phylogenetic analyses*

Based on the phylogenetic inference from the Bayesian and ML analyses of the four mtDNA sequence alignments,

**Table 2.** Data sets and nucleotide substitution models.

| Data set | AL | No.S | No.H | No.VS/No.PIS | ML[b] | Bayesian[b] |
|---|---|---|---|---|---|---|
| D-Loop+cytb+COII+PAST | 4826 | 91 | 77 | 1550/1440 | TVM+I+G | GTR+I+G |
| cytbGB | 1140 | 216 | 98 | 384/348 | GTR+I+G | GTR+I+G |
| COIIGB | 684 | 139 | 55 | 191/170 | GTR+I+G | GTR+I+G |
| CFTR-PAIRB+FIBA+vWF | 2337 | 91 | [a] | 163/120 | GTR+I+G | GTR+I+G |
| FIBAGB | 606 | 208 | [a] | 45/30 | TVM+I+G | GTR+I+G |
| vWFGB | 795 | 208 | [a] | 108/80 | HKY+I+G | HKY+I+G |

Note: AL, Alignment length including outgroup; No.S, Number of sequences in data set excluding outgroup; No.H, number of haplotypes excluding outgroup; [a]only for mitochondrial DNA; No.VS and No. PIS, number of variable site and number of parsimony informative sites, respectively, excluding outgroup; [b]Nucleotide substitution models for each data set.

four major *Cheirogaleus* subgroups were represented, which correspond to the four species *C. crossleyi*, *C. major*, *C. medius* and *C. sibreei* (Figs. 2–3; Appendix I(a)). All of these subgroups were strongly supported (ML BP = 100 and Bayesian PP > 0.99). Cytb was used by all the previously published data, and the results of analyses did not vary based on data type, so for expediency we will use cytb for subsequent analyses and discussions.

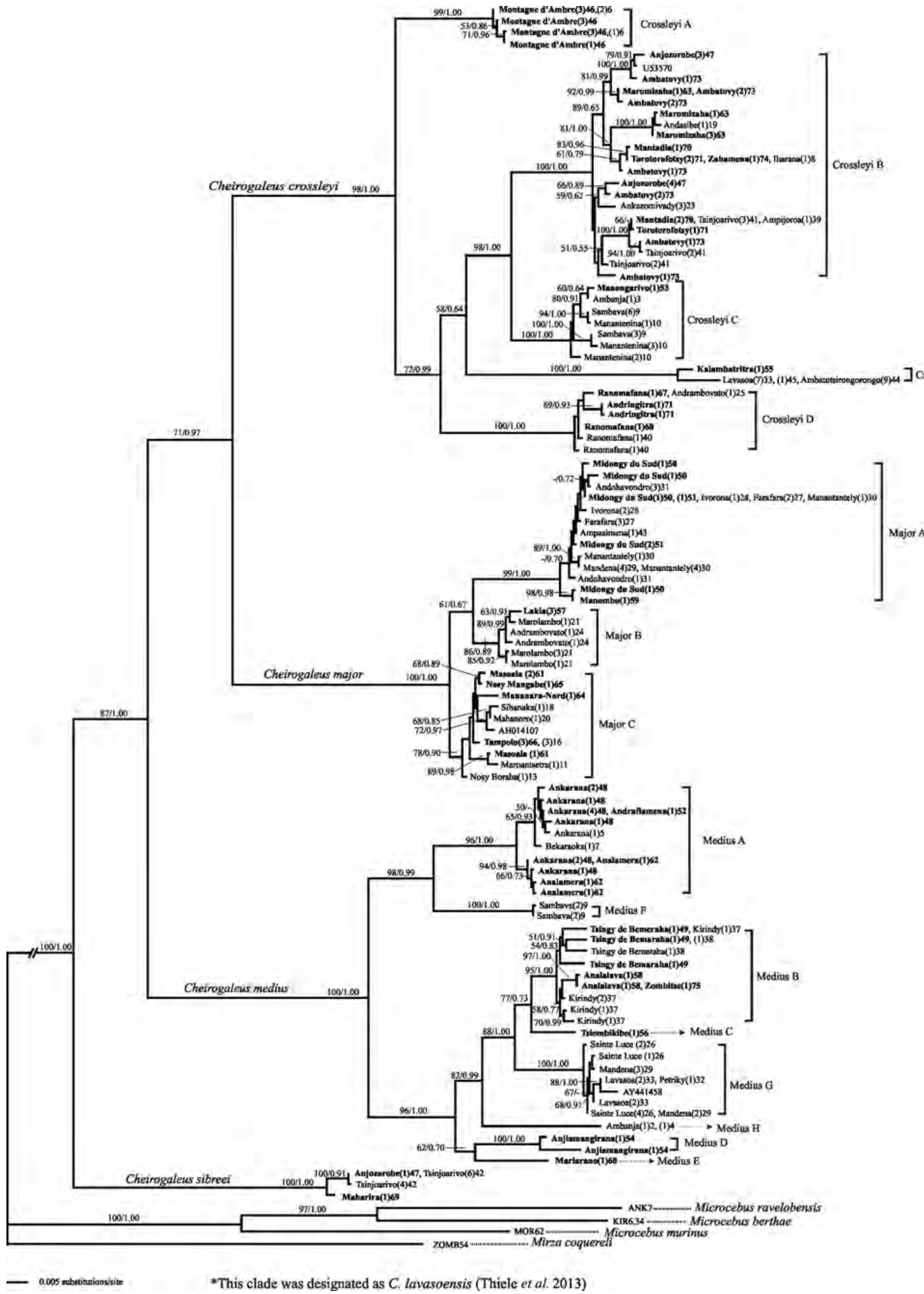
*Cheirogaleus sibreei* formed a distinct clade with high support values (ML BP = 100 and Bayesian PP = 1.00), which contains mtDNA haplotypes from Tsinjoarivo (Vatateza), Anjozorobe and Maharira in Ranomafana National Park. There are more than 180 km of continuous high altitude forest between Tsinjoarivo and Maharira and 130 km of continuous high altitude forest between Tsinjoarivo and Anjozorobe, expanding the possible known range of this species. Additional research in this corridor could provide confirmation of a continuous extended range.

The *C. crossleyi* subgroup contained five distinct clades (Crossleyi A–E) with high support values (ML BP > 99 and Bayesian PP = 1.00). Crossleyi A was composed of mtDNA haplotypes from the northern tip of Madagascar (Montagne d'Ambre, localities 6 and 46). Crossleyi B contained haplotypes from eastern Madagascar (from Tsinjoarivo to Zahamena) and Iharana, a site whose exact locality was unknown in northern Madagascar but may be Vohemar (Falling Rain Genomics, Inc. 2014). A sample from Ampijoroa (locality 39) in western Madagascar was also included, but only 300 bp of data were available, making its placement in the tree possibly a result of missing data rather than a reflection of its true relationship. Crossleyi C had haplotypes from northern Madagascar (localities 3, 9, 10, and 53). Crossleyi D was composed of mtDNA haplotypes from southeastern Madagascar (localities 40, 67, 68 and 71). Crossleyi E contained mtDNA haplotypes from the southeastern tip of Madagascar (localities 33, 44, and 45) and one from Kalambatritra. Uncorrected p-distances based on the complete mtDNA cytb sequence data were calculated and presented in Appendix II(g). The genetic distances were from 5.6–8.1% between Crossleyi A and Crossleyi B–E. Compared with Crossleyi B and Crossleyi A, C–E, there were 4.2–8.3% sequence divergence. Similarly, there are 4.2–7.7%, 6.0–8.2%, 7.7–8.3% between Crossleyi C and Crossleyi A–B, D–E, between Crossleyi D and Crossleyi A–C, E, between Crossleyi E and Crossleyi A–D, respectively.

The *C. major* subgroup included three distinct clades (Major A–C). Major A was strongly supported (ML BP = 99 and Bayesian PP = 1.00) and was composed of mtDNA haplotypes from southeastern Madagascar (Localities 27–31, 43, 44, 50, 51 and 59). Major B had a ML BP value of 86 and a Bayesian PP of 0.89, including haplotypes from central-eastern Madagascar (Localities 21, 24 and 57). Major C had a ML BP value of 78 and a Bayesian PP of 0.90, containing mtDNA haplotypes from central-eastern and northeast Madagascar (Localities 11, 13, 16, 18, 61 and 64–66). The genetic distances in the complete cytb fragment (Appendix II(g)) were from 3.2–3.6% between Major A and Major B–C. Compared with Major B and Major A and C, there was 2.2–3.2% sequence divergence. Similarly, there was 2.2–3.6% sequence divergence between Crossleyi C and Crossleyi A–B.

The *C. medius* subgroup included eight distinct clades (Medius A–H). Medius C, D, E, F and H have single localities such as Tsiombikibo, Anjiamangirana, Mariarano, Sambava and Ambanja, respectively. Medius B was strongly supported (ML BP = 95 and Bayesian PP = 1.00), which contained mtDNA haplotypes from Zombitse to Tsingy de Bemaraha (Localities 37, 38, 49, 58 and 75). Medius G was highly supported (ML BP = 100 and Bayesian PP = 1.00), composed of mtDNA haplotypes from the southeastern tip of Madagascar (Localities 26, 29, 32, and 33). Medius A formed a distinct clade with a high support value (ML BP = 96 and Bayesian PP = 1.00), with mtDNA haplotypes from Ankarana to Andrafiamena (Localities 5, 7, 26, 29, 32, and 33). The genetic distances of the complete cytb fragment (Appendix II(g)) were from 4.7–8.0% between Medius A and Medius B–H. Compared with Medius B and Medius A and C–H, there was 2.1–7.2% sequence divergence. Similarly, there was 3.1–7.7% sequence divergence between Crossleyi G and Crossleyi A–F and H.

Based on Figure 4, all mtDNA published sequences from museum samples of *C. major* were clustered in clade Major C. The mtDNA published sequence from a museum sample of *C. crossleyi* was included in clade Crossleyi B. The mtDNA published sequences from museum samples of *C. medius* were placed in clade Medius B. A mtDNA published sequence from a single museum sample (#1967-1655) of *C. medius* was placed in clade Medius E, which is geographically close to



*This clade was designated as *C. lavasoensis* (Thiele *et al.* 2013)

**Figure 2.** Phylogenetic relationships between *Cheirogaleus* species inferred from the maximum likelihood and Bayesian approaches of the complete cytb sequence data (1140 bp) generated from the 225 *Cheirogaleus* individuals with four out-group taxa. New field samples were labeled in bold. Numbers on branches represent maximum likelihood values followed by posterior probability support. Tip labels include locality, followed by number of individuals carrying the haplotype in brackets, then the locality numbers.

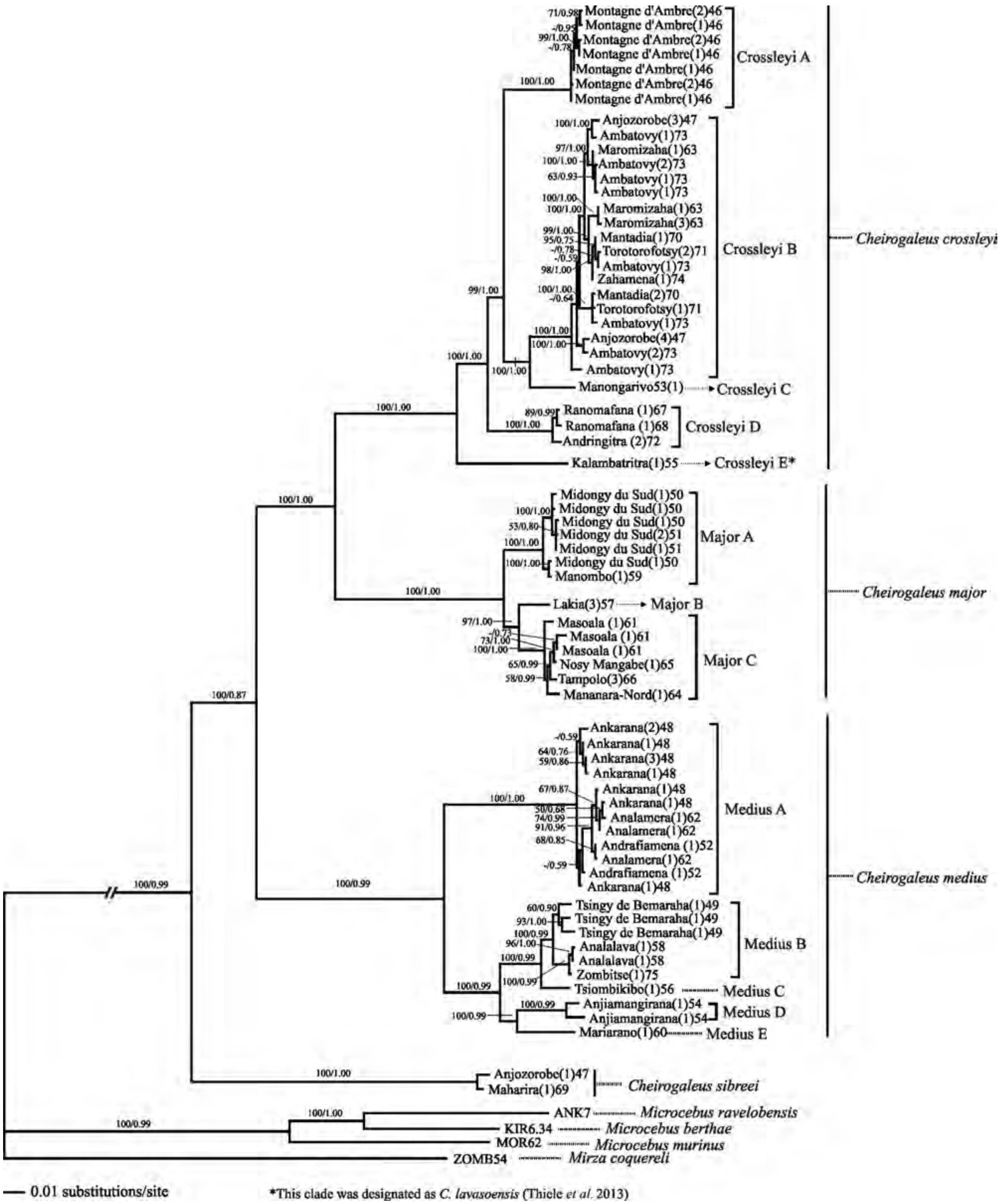
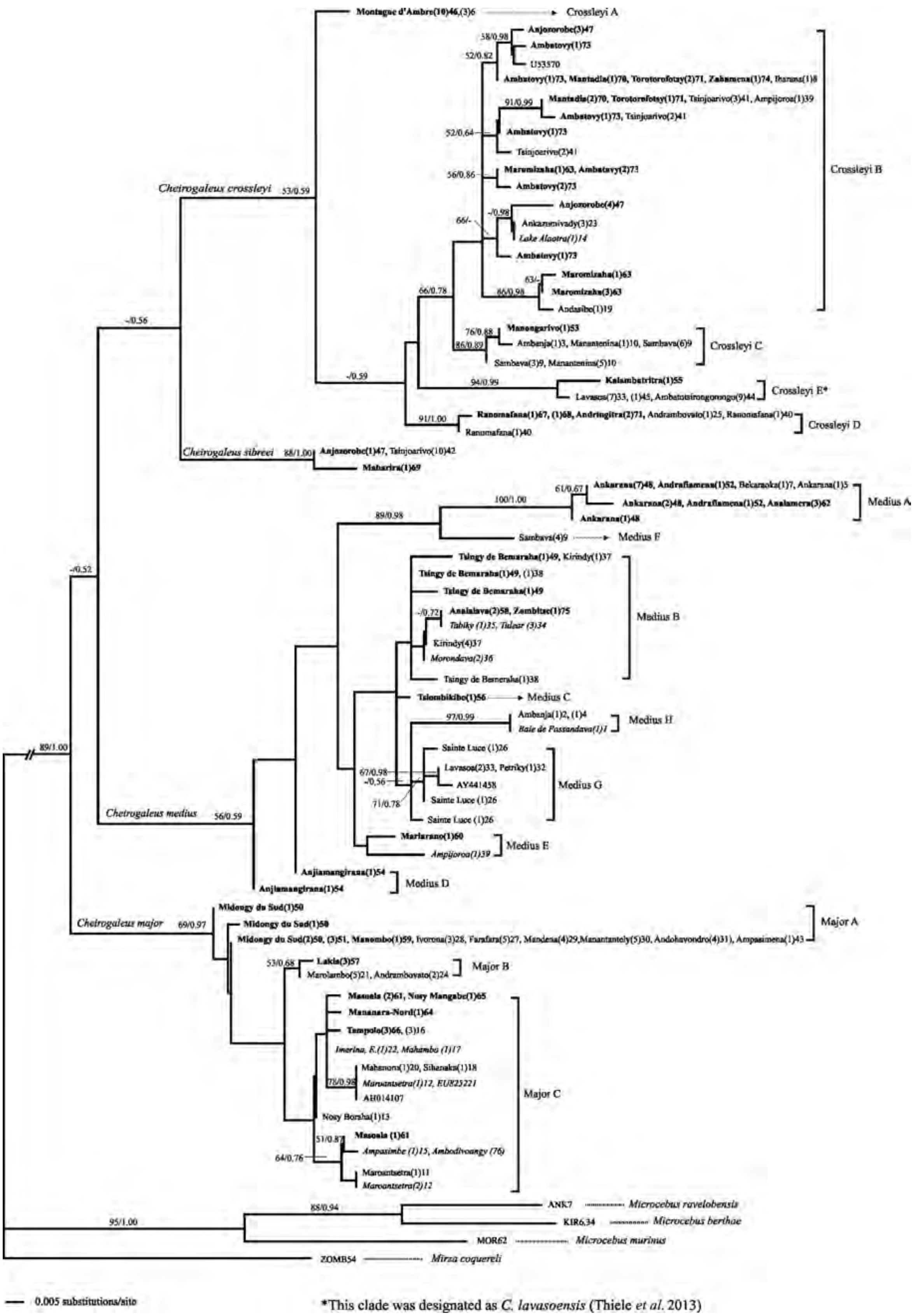


**Figure 3.** Phylogenetic relationships between *Cheirogaleus* species inferred from the maximum likelihood and Bayesian approaches of D-loop, cytb, COII and PAST combined sequence data (4826 bp) generated from the 91 *Cheirogaleus* individuals with four out-group taxa. Numbers on branches represent maximum likelihood values followed by posterior probability support. Tip labels include locality, followed by number of individuals carrying the haplotype in brackets, then the locality numbers.



*This clade was designated as *C. lavasoensis* (Thiele *et al.* 2013)

**Figure 4.** Phylogenetic relationships between *Cheirogaleus* species inferred from the maximum likelihood and Bayesian approaches of the partial cytb sequence data (246 bp) generated from the 242 *Cheirogaleus* individuals with four out-group taxa. Sequences generated from new field samples were labeled in bold and published sequences derived from museum specimens were presented in italic. Numbers on branches represent maximum likelihood values followed by posterior probability support. Tip labels include locality, followed by number of individuals carrying the haplotype in brackets, then the locality numbers.

its sister taxon (Fig. 1). A mtDNA published sequence from another single museum sample (#1887:66b) of *C. medius* was placed in clade Medius H, which is geographically close to its sister taxa (Fig. 1).

Based on the phylogenetic inference from the Bayesian and ML analyses of the three nucDNA sequence alignments, four major *Cheirogaleus* subgroups were strongly supported (ML BP = 100 and Bayesian PP > 0.98), which were congruent to phylogenetic analyses based on mtDNA data (Fig. 5; Appendices I(b–c)). However, in contrast to forming distinct clades and strong phylogeographic structures and harboring extremely divergent haplotypes as in the mtDNA data set, only Medius A formed a clade with distinct subdivisions. There were no distinct clades, and alleles were shared among populations, even with a geographic distance of more than 900 km (Fig. 5; Appendices I(b–c)). The incongruence may be due to ancient introgression, incomplete lineage sorting, or insufficient nucDNA data.

In the two Bayesian species tree analyses, ESS for all factors was greater than 200. *Cheirogaleus crossleyi*, *C. major*, *C. medius* and *C. sibreei* formed strongly supported monophyletic groups (Fig. 6). The relationships among subgroups were incongruent between analyses.

### *Population aggregate analyses*

The results of the PAA of all the sequence data were presented in Appendices II(n–t). In the clade Crossleyi A, there were four diagnostic sites in cytb, nine in PAST, five in D-loop and two in COII. In the clade Crossleyi D, there were six diagnostic sites in cytb, 13 in PAST, two in D-loop and one in COII. In the clade Major A, there were three diagnostic sites in cytb, eight in PAST, none in D-loop and two in COII. In the clade Major C, there were two diagnostic sites in cytb, two in PAST, one in D-loop and none in COII. In the clade Medius A, there were five diagnostic sites in cytb, 36 in PAST, 13 in D-loop and one in COII. In the clade Medius B, there were three diagnostic sites in cytb, one in PAST, none in D-loop and none in COII. In the clade Medius G, there were four diagnostic sites in cytb. For these clades, there were no diagnostic sites found in the three nuclear gene sequence data sets.

### *Morphometric data*

The mean and standard deviation of the morphometric data for each clade of dwarf lemurs are presented in Appendix I(d), and Appendices II(b–c, u) (see Table 4). No extensive quantitative and comparative analyses were conducted on the morphometric data because of numerous factors such as small sample sets, independent data sets, multiple data collectors, the variance between live individuals versus processed museum vouchers, along with seasonal and age differences of individual dwarf lemurs. Therefore, morphometric information was provided as supplemental data only.

### *Taxonomy of Cheirogaleus*

Combining the information from previous studies and the new results obtained here, the taxonomy of *Cheirogaleus* was elucidated, including six nominal species of *Cheirogaleus* (excluding *C. minusculus*), seven CCS, and four UCS. The described species and undescribed forms, and the associated morphological and geographical data assessed in this study are summarized in Tables 3 and 4. The geographical distribution of accepted species, CCS and UCS in the genus *Cheirogaleus* are presented in Figure 7. Localities of museum specimens were georeferenced when possible for historical information on distributions; see Appendix II(d) for institutes of deposit, localities and determination histories.

## Discussion

### *Species concepts*

Increasingly powerful computational and laboratory tools have made ever more complex genomic analyses (Baker 2010) possible and pushed the boundaries of species definitions outside the realm of Mayr's (1942) Biological Species Concept (BSC). The BSC states that sympatric reproductive isolation is the hallmark of a species. The PSC (Eldredge and Cracraft 1980; Wheeler and Platnick 2000) grew out of the early work of Hennig (1965) and provides a methodology for species description more suitable to the era of genomics, allowing new species to be described based on fixed variations in sequence data, and proposing the monophyly of a species as a criterion. Descriptions of new lemur species have partly relied on this concept to justify the elevation of often phenotypically similar animals to species status (Louis *et al.* 2006; Radespiel *et al.* 2012; Rasoloarison *et al.* 2013; Thiele *et al.* 2013). Relying on fixed genetic characters as markers has now become an accepted methodology for the delineation of new species (Schuh and Brower 2009; Louis and Lei 2014).

### *Historical and contemporary taxonomy*

Genetic analyses indicate that the morphologically variable and widespread species, *C. major*, *C. medius* and *C. crossleyi*, harbor previously uncharacterized diversity (Thiele *et al.* 2013). The recent description of *C. lavasoensis* addressed this in part, but resulted in a polyphyletic *C. crossleyi* at odds with the PSC (Thiele *et al.* 2013). To support the continued recognition of this new species, there must be agreement on which lineages represent *C. crossleyi*, *C. major* and *C. medius sensu stricto*. To address this need, we link these names to their respective clades and provide additional support for *C. sibreei* and *C. lavasoensis*, which were already corroborated with genetic evidence (Groeneveld *et al.* 2009, 2010; Thiele *et al.* 2013). Summaries of genetic and historical data are provided in the species descriptions (see below). The remaining unnamed lineages complemented with sufficient evidence can now be elevated to species status.

*Cheirogaleus* does not appear to have undergone as large of a radiation as *Microcebus*, but our molecular analyses indicate that the number of described species is still well below the probable total (Schmid and Kappeler 1994; Zimmermann *et al.* 1998; Rasoloarison *et al.* 2000, 2013; Kappeler *et al.* 2005; Louis *et al.* 2006; Olivieri *et al.* 2007; Radespiel *et al.*

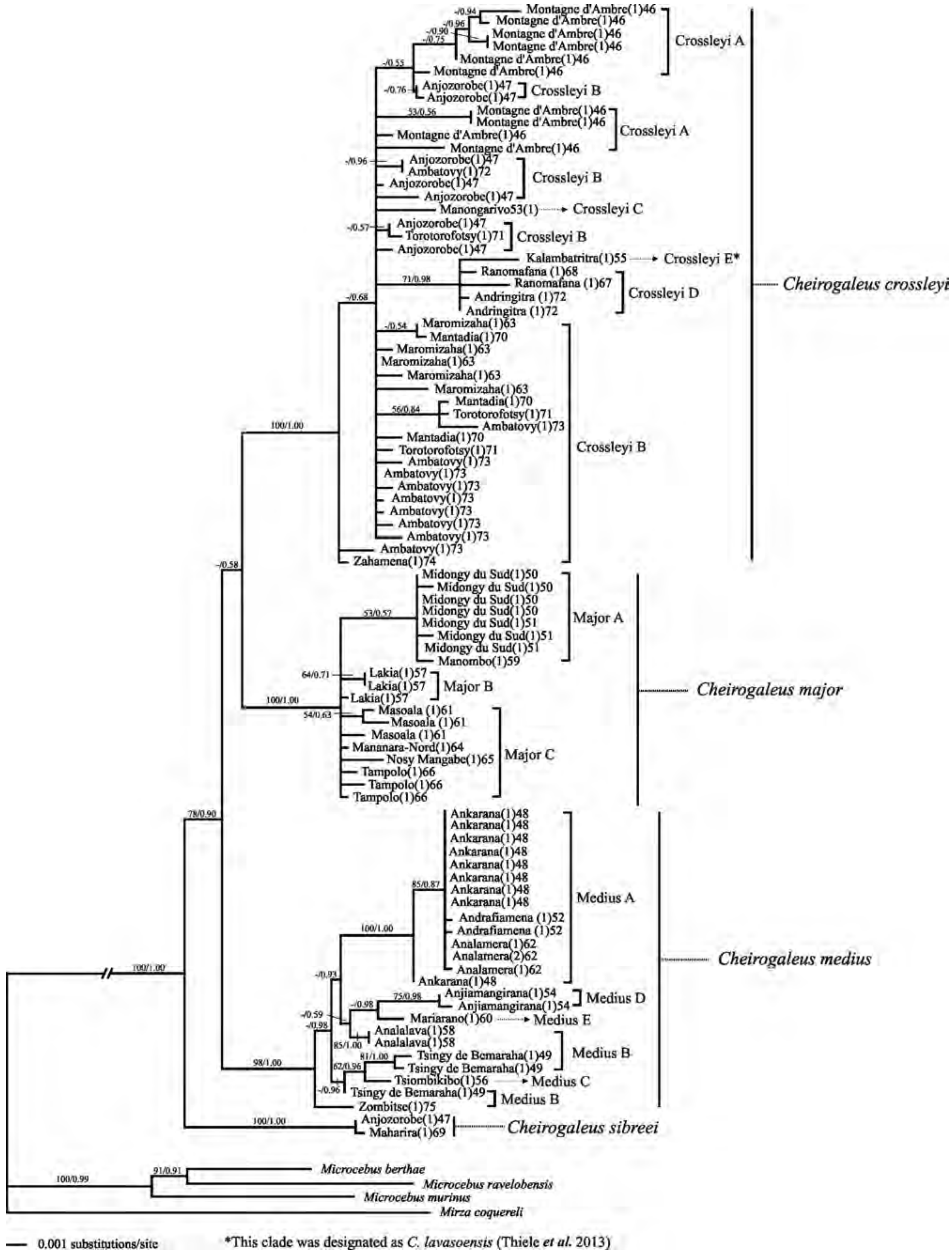


**Figure 5.** Phylogenetic relationships between *Cheirogaleus* species inferred from the maximum likelihood and Bayesian approaches of CFTR-PAIRB, FIBA, and vWF combined sequence data (4826 bp) generated from the 91 *Cheirogaleus* individuals with four out-group taxa. Numbers on branches represent maximum likelihood values followed by posterior probability support. Tip labels include locality, followed by the number of individuals carrying the haplotype in brackets, then the locality numbers.

2008, 2012). We followed the designation criteria of earlier studies (Vieites *et al.* 2009; Padial *et al.* 2010) and adopted the nomenclature of Ratsoavina *et al.* (2013) to distinguish between lineages that require additional information to confirm species status (UCS) and those that currently have sufficient evidence to be described as species (CCS). This study of Malagasy leaf-tailed geckos (genus *Uroplatus*) is particularly pertinent to our work with *Cheirogaleus*, as both lineages contain widespread phenotypically similar taxa with large mtDNA sequence divergence between species.

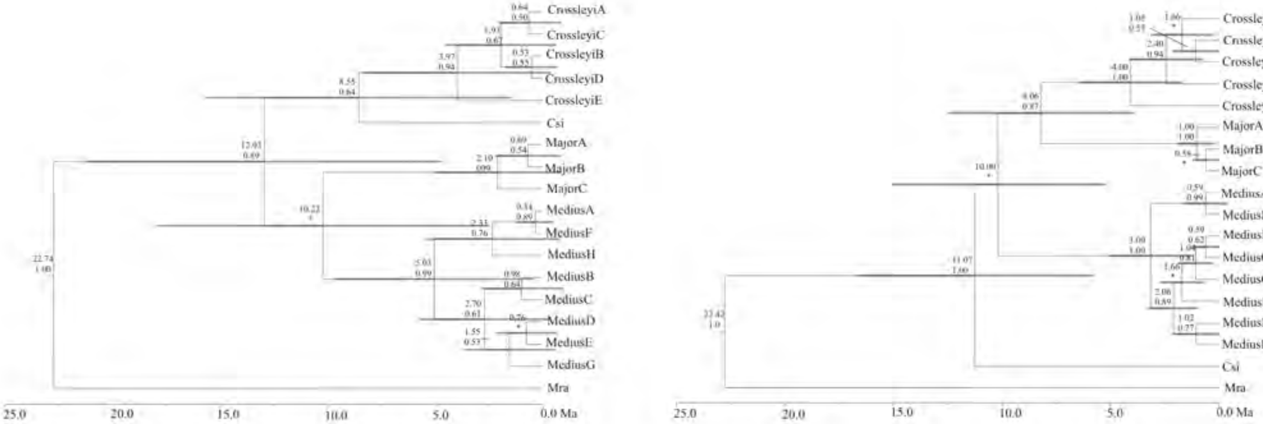


**Figure 6.** Maximum clade credibility phylogeny of the genus *Cheirogaleus* inferred by the *BEAST species tree analyses of nuclear genes (A) and a combined nuclear gene and mtDNA datasets (B) with *Microcebus ravelobensis* (Mra) as outgroup. Node labels: estimated divergence time (Ma) and posterior probabilities (≥ 0.5; * stands for < 0.5). Node bars indicate the 95% interval of divergence time estimates with posterior probabilities.

**Table 3.** History of accepted *Cheirogaleus* species included in published genetic investigations and the most recent morphological study (Groves 2000) correlated with clades identified in this study. New candidate species are also identified. Notations: n.i. = not included or not explicitly mentioned in the respective paper; CCS = confirmed candidate species; USC = unconfirmed candidate species.

| Species | Clade | Hapke *et al.* (2005) | Groeneveld *et al.* (2009, 2010) | Thiele *et al.* (2013) | This study |
|---|---|---|---|---|---|
| *C. sibreei* | *C. sibreei* | n.i. | *C. sibreei* | *C. sibreei* | *C. sibreei* |
| *C. ravus* | n.i. | n.i. | *C. major* | n.i. | *C. major* |
| *C. minusculus* | n.i. | n.i. | n.i. | n.i. | *C. minusculus*[a] |
| *C. crossleyi* | Crossleyi A | *C. crossleyi* | *C. crossleyi* | *C. crossleyi* | CCS1 |
| | Crossleyi B | *C. crossleyi* | *C. crossleyi* | *C. crossleyi* | *C. crossleyi* |
| | Crossleyi C | *C. crossleyi* | *C. crossleyi* | *C. crossleyi* | CCS2 |
| | Crossleyi D | *C. crossleyi* | *C. crossleyi* | *C.* sp. Ranomafana Andrambovato | CCS3 |
| *C. lavasoensis* | Crossleyi E | *C. crossleyi* | *C. crossleyi* | *C. lavasoensis* | *C. lavasoensis* |
| *C. major* | Major A | *C. major* | *C. major* | *C. major* | CCS4 |
| | Major B | *C. major* | *C. major* | *C. major* | CCS5 |
| | Major C | *C. major* | *C. major* | *C. major* | *C. major* |
| *C. medius* | Medius A | *C. medius* | *C. medius* | *C.* sp. Bekaraoka Sambava | CCS6 |
| | Medius B | *C. medius* | *C. medius* | *C. medius* | *C. medius* |
| | Medius C | n.i. | n.i. | n.i. | UCS1 |
| | Medius D | n.i. | n.i. | n.i. | UCS2 |
| | Medius E | n.i. | n.i. | n.i. | UCS3 |
| | Medius F | n.i. | *C. medius* | *C.* sp. Bekaraoka Sambava | CCS7 |
| | Medius H | n.i. | *C. medius* | *C.* sp. Ambanja | UCS4 |
| *C. adipicaudatus* | Medius G | n.i. | *C. medius* | *C. medius* | CCS8 |

[a] Data Deficient

The identification of seven CCS and four UCS vastly expands the possible circumscription of *Cheirogaleus* (Table 3). The distribution of proposed taxa resembles that of the nocturnal *Lepilemur* group (Louis *et al.* 2006), with numerous pockets of diversity in the North, Northwest 1, and Northwest 2 biogeographic regions marked by the presence of rivers that appear to act as gene flow barriers (Louis and Lei in press). In contrast, speciation in southern Madagascar may be driven more by the convoluted intersection of three biogeographic regions, Central Highlands, West 2 and East 2, associated with rapidly shifting climatic and geological characteristics across a short geographic distance. In this area, near the city of Tolagnaro (Ft. Dauphin), there are three *Cheirogaleus* species, all of which may be sympatric (Fig. 7).

Five clades demonstrated sufficient genetic differentiation (PAA) via our use of multiple genetic analyses, along with sufficient geographic distance or barriers (ascertained by examining maps of Madagascar) from other species to warrant their elevation as four new and one resurrected species. Within the Crossleyi group, CCS1, found in proximity to Montagne d'Ambre, was elevated to full species status as *Cheirogaleus* **species nova 1**. CCS3 has been elevated to species status as *C.* **species nova 2.** Of the Major subgroups, CCS4 has been elevated to species status as *C.* **species nova 3.** CCS6 from the Medius lineage has been elevated to species status as *C.* **species nova 4**. Additionally, we resurrected *C. thomasi*, described by Forsyth Major (1894) as *Opolemur thomasi*, for CCS8. This species was initially described from Tolagnaro (Ft. Dauphin) by Forsyth Major (1894), but synonymized with *C. medius* by Schwarz (1931). Our study indicates the presence of an unnamed lineage here, and based on the principle of priority in species naming of the International Code of Zoological Nomenclature (ICZN), the available name is *C. thomasi* (see below).

In the case of CCS2, 5, and 7 additional sampling and physical examinations from wild populations need to be

**Table 4.** Summary of preliminary morphometric data and collection localities of species and candidate *Cheirogaleus* species, with information merged for male and female adult specimens (juveniles were excluded). Data are preliminary, and details will be reported in forthcoming revisions. W: weight, HC: head crown, BL: body length, TL: tail length; ( ) number of genetic samples.

| Species and candidate species | Morphological characters | | | | Altitude range (m) | Collection localities | Specimens examined |
|---|---|---|---|---|---|---|---|
| | W (kg) | HC (cm) | BL (cm) | TL (cm) | | | |
| *C. sibreei* | 0.23±0.00<br>0.27±0.04[a] | 7.0±1.4<br>- | 15.4±1.2<br>- | 23.1±0.6<br>23.5±1.3[a] | 1128–1660 | Tsinjoarivo (Andasivodihazo), Anjozorobe, Maharira | 2 (12) |
| *C. minusculus* | - | - | - | - | 1678 | Ambositra | - |
| CCS1 | 0.31±0.04 | 5.9±0.3 | 17.6±0.8 | 26.3±2.1 | 541–1073 | Montagne d'Ambre | 9 (13) |
| *C. crossleyi* | 0.33±0.07 | 6.0±0.7 | 18.6±1.4 | 26.5±2.2 | 856–1535 | Ambatovy, Andasibe, Anjozorobe, Ankazomivady, , Mantadia, Maromizaha, Torotorofotsy, Tsinjoarivo, Zahamena, | 26 (43) |
| CCS2 | 0.32±0.10 | 5.7±0.2 | 16.8±2.0 | 26.6±1.5 | 18–303 | Ambanja, Manantenina, Manongarivo, Sambava, | 8 (9) |
| CCS3 | 0.41±0.12<br>0.37±0.04[a] | 6.3±0.6<br>- | 20.1±3.8<br>- | 27.7±2.8<br>27.7±1.3[a] | 754–999 | Andrambovato, Andringitra (Ambarongy), Ranomafana (Talatakely), Ranomafana (Vatoharanana), | 4 (5) |
| *C. lavasoensis* | 0.27+0.00<br>0.27+0.02[b] | 6.9±0.0<br>- | 16.0±0.0<br>- | 24.9±0.0<br>25.1±0.1[b] | 300–1223 | Petit Lavasoa, Ambatotsirongorongo, Grand Lavasoa, Kalambatritra (Sahalava) | 1 (18) |
| CCS4 | 0.46±0.13 | 6.4±0.5 | 19.3±2.0 | 28.4±1.2 | 17–789 | Ambatotsirongorongo, Ampasimena, Andohavondro, Farafara, Ivorona, Manantantely, Mandena, Manombo, Midongy du Sud, | 8 (31) |
| CCS5 | - | - | - | - | 85–763 | Lakia, Marolambo, Andrambovato | 0 (10) |
| *C. major* | 0.34±0.13<br>0.35+0.03[b] | 6.0±0.9<br>- | 19.7±2.8<br>- | 28.1±2.7<br>28.9±1.8[b] | 4–682 | Mahanoro, Mananara-Nord, Maroantsetra, Masoala, Nosy Boraha, Nosy Mangabe, Sihanaka, Tampolo, | 5 (13) |
| CCS6 | 0.09±0.03 | 3.9±0.5 | 11.6±2.0 | 14.4±2.1 | 10–292 | Ankarana, Andrafiamena, Analamera, Bekaraoka | 4 (16) |
| *C. medius* | 0.23±0.06 | 4.9±0.3 | 13.8±0.6 | 20.2±2.4 | 60–801 | Analalava, Kirindy, Tsingy de Bemeraha, Zombitse | 6 (11) |
| UCS1 | 0.15±0.00 | 4.5±0.0 | 12.0±0.0 | 12.2±0.0 | 15 | Tsiombikibo | 1 (1) |
| UCS2 | 0.23±0.03 | 5.1±0.5 | 15.8±0.6 | 23.5±2.5 | 59–346 | Anjiamangirana | 2 (2) |
| UCS3 | 0.17±0.00 | 4.4±0.0 | 15.9±0.0 | 21.5±0.0 | 53 | Mariarano | 1 (1) |
| CCS7 | - | - | - | - | 18 | Sambava | 0 (4) |
| UCS4 | - | - | - | - | 0–35 | Ambanja | 0 (2) |
| CCS8 | - | - | - | - | 9–320 | Sainte Luce, Lavasoa, Petriky | 0 (18) |

[a]Blanco *et al.* (2009); [b]Thiele *et al.* (2013); -means data deficient

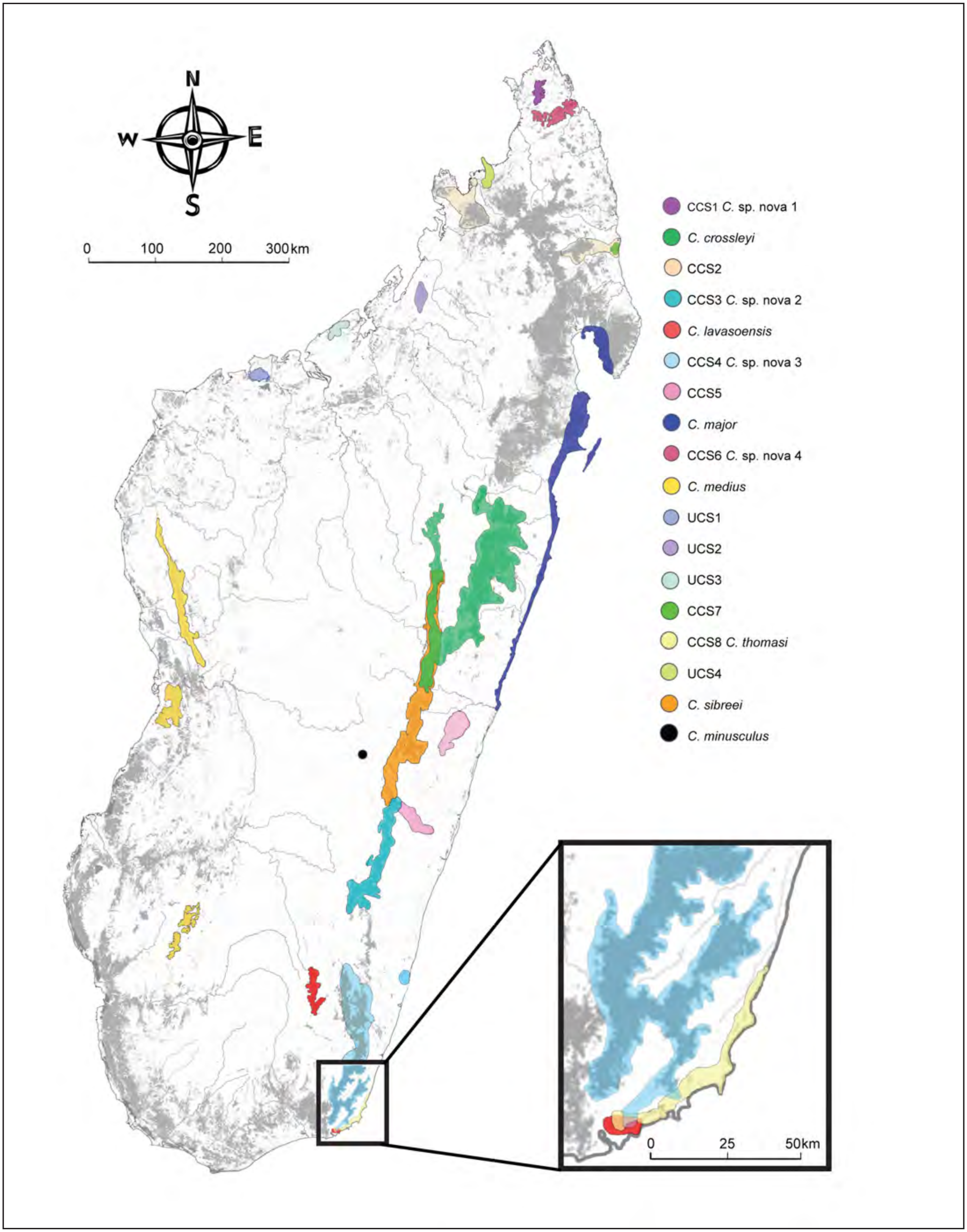


**Figure 7.** Proposed distributions of the dwarf lemurs of Madagascar. Geographic distribution of designated species, CCS, and UCS in the genus *Cheirogaleus*, with suspected ranges denoted by colors.

conducted to scientifically name these lineages with full confidence. Further, our CCS were all identified by previous studies as members of recognized species groups. A large amount of evidence for these three CCS is extant, but complicating factors exist in proposing a scientific name at this time. CCS2, for instance, is known from 17 genetic samples in northern Madagascar from the east and west coasts (localities 3, 9, 10, and 53). These collection localities represent very different habitats and are in separate biogeographic zones (Louis and Lei in press). Without additional fieldwork in forests between these locales, it is not possible to be certain of the monophyly of CCS2 until additional sampling is completed.

In the case of UCS1–4, we strongly suspect the possibility of independent species due to genetic and geographical factors, but lack the evidence at present to elevate them to species status. Furthermore, temporal climatic variation resulting in the expansion and contraction of forest also contributed to these speciation events (Wilmé *et al.* 2006). UCS1, for instance, is known from one specimen examined at Tsiombikibo (Locality 56) in western Madagascar. Genetic data collected from this individual, coupled with the geographic distance from other *C. medius* populations, indicates a probable but unconfirmed candidate species. UCS2 is known from two individuals sampled at Anjiamangirana (Locality 54), another isolated habitat separate from other *C. medius* populations. UCS3 is known from one individual examined and sampled at Mariarano (Locality 60). Only UCS4 was recognized in a previous study; UCS4 is known from two genetic samples collected at Ambanja (Localities 2 and 4). Groeneveld *et al.* (2009) identified UCS4 as *C. medius*, while Thiele *et al.* (2013) identified UCS4 as a probable new species, *C.* sp. Ambanja, but declined to complete the identification with a formal taxonomic name. Additional field and laboratory work is needed to confirm the status of UCS1–4.

All four of these UCS are endemic to northwestern Madagascar, where rivers serve as barriers that isolate populations already under intense pressure from deforestation and other human activities such as hunting, and may be driving speciation. It is particularly notable that a previous study (Louis *et al*. 2006) identified the northwestern part of Madagascar as the region of highest overall species richness for the sportive lemurs (Lepilemuridae). This species richness, with river boundaries a probable contributing factor, appears to be present in *Cheirogaleus* as well.

The elevation of a large number of new lemur species in a relatively short period of time has drawn some criticism and calls for a return to the BSC or a more strict application of the PSC (Tattersall 2007, 2013). We contend that the genetic and geographic evidence justify the elevation of these four new species. Madagascar's geography, including varying altitudes and river barriers, encourage speciation (Louis *et al.* 2006). Increasingly fragmented habitats have left populations isolated, and this situation may further contribute to the speciation events that result in new lineages (Quinn and Harrison 1988). Our identification of four new *Cheirogaleus* species and the probable existence of numerous others are indicative of the work that remains to be done in Madagascar to prevent the ongoing loss of that island's amazing biodiversity.

*Species groups of* Cheirogaleus

Four species groups in this genus are identifiable as follows:

1. *C. crossleyi* group

**External characters**: Characterized by a dark facial mask, consisting of broad black or blackish-grey, usually somewhat angular, rings around the eyes, extending broadly anteromedially to join with the intensely black muzzle. The ears are black and furred inside and out. The general color of the head continues as a lighter strip between the eye-rings and their anteromedial continuations as far as the muzzle. The white or whitish area of the throat continues to the cheeks and muzzle, contrasting somewhat with the color of the face. Dorsal side of the body and posterior of the head reddish-grey. Underside and inner aspects of the limbs white or light grey, forming a sharp border with the color of the upperside, and extending well up on the sides of the neck and onto the cheeks.

**Skull**: Facial skeleton low and straight; a broad interorbital space, not markedly constricted in the middle; orbits looking more laterally; orbital margins not, or bluntly, raised, the upper rims low, not interrupting the dorsal outline of the skull, and the inferior orbital margins hardly anterior to superior margins; orbits looking at about 45° from the front, their rims in a single plane. Lateral walls of the nasals smoothly continuing the upwardly converging slopes of the maxillae. The posterior margin of the palate distinctly curved forward; vomer not strongly prolonged backward, lateral pterygoids not enlarged; bullae relatively small. The lateral margin of the pyriform aperture is somewhat concave in lateral view; the braincase is low, suddenly steeply descending posteriorly (Appendix I(d)).

**Dentition**: Toothrows straight or nearly so, not or only slightly incurved posterior to M2, evenly converging anteriorly; incisor row only slightly curved, incisors slightly project forward; canine short, barely curved and not much protruding above level of P2, and with small distal cusp; P2 relatively low-crowned, barely protruding above level of P3, and separated from both canine and P3 by short diastemata; molar cusps low; P2 and P3 slender, buccolingually compressed; P4 constricted between buccal cusps and lingual cusp; upper molars square; M3 relatively small, but not reduced in structure, its lingual margin nearly symmetrically crescentic.

***Cheirogaleus crossleyi*** (Grandidier, 1870). *Rev. Zool. pur et appliquée* 22: 49.

*Chirogalus crossleyi* Grandidier, 1870

*Chirogale melanotis* Forsyth Major, 1894

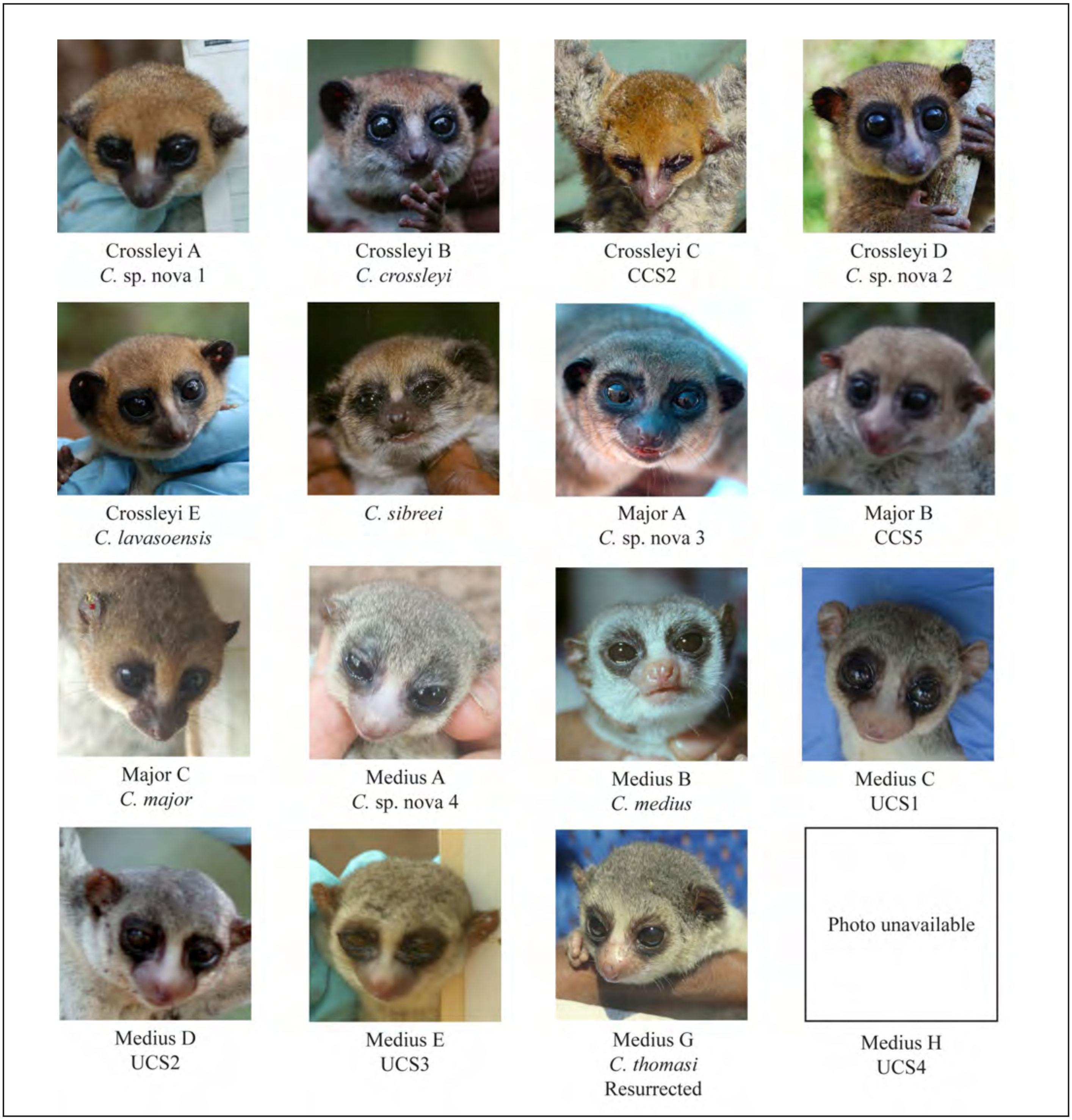
*Summary:* We propose that the clade identified as Crossleyi B represents Grandidier's *C. crossleyi*. This clade includes the museum specimen identified as 1948.160 (BMNH) collected 30 miles northeast of Lac Alaotra (Fig. 4). The characteristic yellow fur on the face (Groves 2000) is visible on an individual from Zahamena (Fig. 8). A type specimen was previously unknown for *C. crossleyi*, but Groves recently discovered it in the collections of the Museum of Comparative Zoology at Harvard University from the Grandidier collection from the Forest of Antsianaka near Lac Alaotra (Viette 1991).

*Holotype*: MCZ 44952, adult female, skin and skull; of *melanotis*, BM 70.5.5.24, adult male, skin and skull.

*Type locality*: Forest of Antsianaka; of *melanotis*, Vohima.

*Distribution*: Known from Zahamena in the north down through Tsinjoarivo in the south in forests along the central high plateau.

*Vernacular names*: Crossley's dwarf lemur, furry-eared dwarf lemur, Matavirambo or Tsitsihy.



Crossleyi A
*C.* sp. nova 1

Crossleyi B
*C. crossleyi*

Crossleyi C
CCS2

Crossleyi D
*C.* sp. nova 2

Crossleyi E
*C. lavasoensis*

*C. sibreei*

Major A
*C.* sp. nova 3

Major B
CCS5

Major C
*C. major*

Medius A
*C.* sp. nova 4

Medius B
*C. medius*

Medius C
UCS1

Medius D
UCS2

Medius E
UCS3

Medius G
*C. thomasi*
Resurrected

Photo unavailable

Medius H
UCS4

**Figure 8.** Photographs of living specimens in the genus *Cheirogaleus*. A photograph was not available for Medius H UCS4.

***Cheirogaleus* sp. nova 1.** New species

Formerly CCS1; identified as a subclade of *C. crossleyi* by Thiele *et al*. (2013). See Table 3.

***Cheirogaleus* sp. nova 2.** New species

Formerly CCS3; identified as *Cheirogaleus* sp. Ranomafana Andrambovato by Thiele *et al.* (2013). See Table 3.

***Cheirogaleus lavasoensis*** Thiele, Razafimahatratra & Hapke, 2013. *Mol. Phylogenet. Evol.* 69: 605.

*Holotype*: IFA AH-X-00-181, DNA and tissue from an adult male, subsequently released (Thiele *et al.* 2013).

*Type locality*: Madagascar, Region Anosy, Lavasoa Mountains, a forest fragment locally named Bemanasy, on the southern flank of Petit Lavasoa, S 25.080894, E 46.762151, at 300 m above sea level (Thiele *et al.* 2013).

*Diagnosis*: Intensely reddish coloration on the head; relatively long, wide ears; higher facial skeleton and more reduced third upper molars than other members of the group.

*Description*: Relatively small in size, with a deeper face; upper third molars small.

*Distribution*: From Kalambatritra (this study) in the north down to three small forest fragments on the southern slopes of the Lavasoa Mountains (Thiele *et al.* 2013).

*Vernacular name*: Lavasoa Dwarf Lemur.

***Cheirogaleus crossleyi* group, other potential species**

1) Potential species from Bongolava (no currently existing specimens available for study): Thalmann (2007) and personal communication to C. P. Groves. The photos show a very dark species of the *crossleyi* group, with very large, intensely black eye-rings which leave only a very narrow interorbital space and narrow space between them and the ears. The skull measurements given by Thalmann (2007) indicated an extremely small size, which contradicted external measurements, suggesting further investigation is necessary.

2) CCS2: Representatives of this candidate species were sampled from the east and west coasts in the north of Madagascar (Thiele *et al.* 2013). This lineage was genetically distinct, but before it can be confidently described, the forests between the disjunct collection localities need to be sampled to confirm or exclude gene flow.

2. *C. major* group

**External characters**: Facial mask much less developed, eye-rings more rounded than in *C. crossleyi* group, and less broadly connected to the (usually dark) grey muzzle. Interorbital strip short and broad. Ears somewhat darker than head, but thinly haired. Body and head lighter reddish-grey. Underparts light grey or white, but this color not sharply marked off from that of upper parts.

**Skull**: Facial skeleton short, high, straight; interorbital space narrow; orbital margins (not the rims themselves) bluntly raised; inferior orbital margins well anterior to superior margins; orbits looking at about 45° from the front, their rims in a single plane; orbit enlarged, slightly interrupting the dorsal outline of the skull, extending inferiorly below the level of the zygomatic arch; lacrimal region concave in front of the orbital margin and below the posterior nasals; lateral margin of the pyriform aperture usually straight in lateral view; the nasal tip short, hardly extending anterior to the pyriform aperture margin in lateral view; rostrum bluntly rounded anteriorly, and premaxillae somewhat prolonged forward; the nasals somewhat raised above the maxillae, their lateral walls rising at an angle above the maxillary planes; postorbital constriction deep; temporal lines well-expressed; braincase relatively higher, falling away steeply behind. Posterior margin of the palate much less concave than in *C. crossleyi* group; the vomer still less prolonged than in the latter, but the basisphenoid with a strong median longitudinal ridge; lateral pterygoids small, not flared; bullae small, their inferior margin about level with alveolar line.

**Dentition**: Toothrows mainly straight but curved inward posterior to M2; incisors less forwardly projecting than in *C. crossleyi* group; no canine/P2 diastema, but variably one between P2 and P3; canine thick, curved, but lacking much or any development of distal cusp; P2 and especially P3 broader than in *C. crossleyi* group; P4 oblong in shape; P3 hardly projecting above P4; upper molars square; molar cusps low, bulbous; M3 fairly small in size but not reduced in structure, its lingual margin symmetrically crescentic.

***Cheirogaleus major*** É. Geoffroy Saint-Hilaire, 1812. *Ann. Mus. Hist. Nat. Paris* 19: 172.

*Lemur commersonii* Wolf, 1822 (Renaming of *Cheirogaleus major* É. Geoffroy Saint-Hilaire)

*Cheirogaleus milii* É. Geoffroy Saint-Hilaire, 1828

*Cheirogaleus typicus* Smith, 1833

*Mioxicebus griseus* Lesson, 1840

*Summary*: We propose that the clade identified as Major C represents *C. major sensu* Groves (2000). Unfortunately, there is no type locality for this species, represented by a neotype in the Paris Museum, a specimen that is also the holotype of *Cheirogaleus milii* which was named by É. Geoffroy Saint-Hilaire (1828) on the basis of an individual presented to the Paris Menagerie by Pierre Bernard Milius, Governor of Réunion, and described from life by F. Cuvier (1821). Steven Goodman suggested to C. P. Groves (in litt.) that, at this period, French entry to Madagascar would most likely have been via Tamatave (now Toamasina), so the specimen would most plausibly have been obtained from that vicinity, or between there and Antananarivo. Numerous museum specimens (BMNH: 1939.1289, 1935.1.1or 8.169; MNHN: 1932-3362, 1964.72, 1964.74; NMNL: 1887:66c, 1887:66f, 1887:66g) were included in this clade based on cytb sequences (Fig. 4).

*Types*: Holotype of *milii* and neotype of *major* (and, by implication, of *commersonii* and *griseus*), MNHN148; holotype of *typicus*, BM 37.9.26.77.

*Type locality*: Of *major, commersonii, milii* and *griseus*, probably either Toamasina (formerly Tamatave) or between there and Antananarivo; of *typicus*, "Madagascar".

*Distribution*: Narrow coastal range along the east coast, from Masoala in the north down to Mahanoro River in the south. This littoral habitat is the most threatened in all of Madagascar (Consiglio *et al.* 2006; Watson *et al.* 2010).

*Vernacular name*: Greater dwarf lemur.

***Cheirogaleus* sp. nova 3.** New species

Formerly CCS4; See Table 3.

***Cheirogaleus major* group, other potential species**

1) *Cheirogaleus ravus* Groves, 2000. *Int. J. Primatol.* 21: 960: Although synonymized by Groeneveld *et al.* (2009) based on a partial dataset that did not include the type specimen, this species may represent a distinct lineage. It seems evident that Groves (2000) referred many specimens to this species when described; the type specimen, BM 88.2.18.3, from Toamasina, is unusual, with its very grey color (iron-grey with brownish tones), its short tail with a white tip, braincase less steeply falling away behind, and small M3. The field team has not found any specimen resembling this description. Some of the other specimens referred to *C. ravus* in the type description (Groves 2000) show some, but not all of the putative diagnostic features, for example, an unusually grey color. Therefore, *C. ravus* may be either a distinct species, or simply a highly distinctive morph of *C. major*.

2) CCS5: Representatives of this species were collected from three localities, Lakia (this study), Marolambo and Andrambovato (Groeneveld *et al.* 2009). Additional morphological information is required before this species can be described and additional field work is recommended between these disjunct localities.

3. *C. medius* group

**External characters**: Facial mask poorly developed, eye rings rounded, thin, with barely marked thin lines connecting them to the lateral muzzle; muzzle pinkish-grey. Ears thinly haired, not darker than head. Face contrastingly lighter than the general color of the head. Upperside of the body and head light or medium grey, with tendency for a short dark dorsal stripe and whitish extremities. Underside and inner aspect of the limbs sharply marked-off white, this color extending well up onto the flanks, and sending a striking white "collar" up onto the sides of the neck, leaving often a fairly narrow strip of body color on the upper side of the neck.

**Skull**: Facial skeleton shorter, higher than other groups, becoming convex above the level of the infraorbital foramen; orbits rounded, so that the interorbital space is constricted in the middle, and lateral rims of the orbits turned forward; orbital rims strongly raised; inferior orbital margins well anterior to superior, but the lateral rim is more antero-inferiorly directed, meeting the upper margin of the zygomatic arch at a very acute angle; upper orbital rim slightly interrupting the dorsal outline of the skull. Rostrum narrows anteriorly but its lateral walls somewhat rounded; lateral margin of the pyriform aperture concave in lateral view; nasals somewhat raised above the maxillae, their lateral walls rising at an angle above the maxillary planes. Temporal lines hardly expressed; postorbital constriction is deep; the braincase very low, flat. Posterior margin of the palate strongly concave forward, situated less far behind M3; vomer strongly raised, and prolonged backwards between the pterygoids; lateral pterygoid plates enlarged, flaring; bullae large, constricting basioccipital between them; bullae inflated, they protrude below the alveolar line.

**Dentition**: Toothrows somewhat converging anteriorly, then more strongly curved inward anterior to the canines, and slightly curved inward posterior to M2; incisors less forwardly projecting than in the *C. major* group; canines very long, slender, but barely curved, with a small distal cusp; diastema present between canine and P2, and between P2 and P3; P2 and P3 more rounded, less compressed, with considerable lingual pillars; P2 pointed, high-crowned, projecting well above P3; P4 triangular; molar cusps high and pointed; upper molars more rounded lingually, with a larger protocone; M3 triangular, its distolingual margin reduced.

***Cheirogaleus medius*** É.Geoffroy Saint-Hilaire, 1812. *Ann. Mus. Hist. Nat. Paris* 19: 172.

*Chirogalus adipicaudatus* Grandidier, 1868

*Chirogalus samati* Grandidier, 1868

*Summary*: We propose that the clade identified as Medius B represents *C. medius sensu* Groves (2000). The neotype locality was vaguely described as the Tsidsibon River, which, according to Goodman and Rakotondravony (1996), is currently known as the Tsiribihina River, in west-central Madagascar. Numerous museum specimens were included in this clade based on cytb sequences (1935.1.8.168, 1932-3364, 1932-3365, cat. a/ van Dam a., cat. e/ van Dam e. [Morandava]; Fig. 4). This species is documented from near Toliara, north to Tsingy de Bemaraha. This area, spanning multiple biogeographic regions (Louis and Lei in press), requires additional field work and, based on speciation patterns in other organisms (Louis *et al.* 2006; Ratsoavina *et al.* 2013), will likely reveal new *Cheirogaleus* taxa.

*Types*. Holotype of *samati* and neotype of *medius*, MNHM 162; of *adipicaudatus*, unknown.

*Type localities*: of *medius* and *samati*, Tsidsibon River; of *adipicaudatus*, Tulear (Toliara).

*Distribution*: In western Madagascar, individuals sampled from Tsingy de Bemaraha down to Zombitse. Known from Tsingy de Bemaraha National Park and Zombitse Vohibasia National Park.

*Vernacular name*: Fat-tailed dwarf lemur.

***Cheirogaleus thomasi*** (Forsyth Major, 1894). *Novitates Zoologicae* 1: 20.

*Opolemur thomasi* Forsyth Major, 1894

Formerly, CCS8; *C. adipicaudatus* of Groves (2000), in part.

*Type*: BM 91.11.30.3, skin and skull.

*Type locality*: Fort Dauphin.

*Distribution*: In the southeastern extreme of Madagascar, from St. Luce to Petriky.

*Notes*: Groves (2000) applied the name *C. adipicaudatus* to what is in effect this species, which does not (*contra* Groves) extend throughout the "spiny desert" country of the south of Madagascar.

*Vernacular name*: None known. Suggest Thomas' dwarf lemur.

***Cheirogaleus* sp. nova 4.** New species

Formerly CCS6; in part *C.* sp. Bekaraoka Sambava Thiele *et al.* (2013). See Table 3.

***Cheirogaleus medius* group**: other potential species

1) UCS1: Known from only one individual from one locality, Tsiombikibo. Further investigation of this western, genetically distinct lineage is highly recommended as this geographical area is bounded on its eastern side by the Mahavavy Sud River, which has been shown to be an effective genetic barrier for the genus *Lepilemur* (Louis *et al.* 2006).

2) UCS2: Known from only one individual from one locality, Anjiamangirana. Further investigation of this western genetically distinct lineage is highly recommended as this geographical area is bounded by the Mahajamba and Sofia rivers, which have been shown to be effective genetic barriers for the genus *Lepilemur* (Louis *et al.* 2006).

3) UCS3: Known from only one individual from one locality, Marirano. Further investigation of this western genetically distinct lineage is highly recommended as this geographical area is bounded by the Sofia and Betsiboka rivers, which have been shown to be effective genetic barriers for the genus *Lepilemur* (Louis *et al.* 2006).

4) CCS7: Known from four samples from Sambava (Groeneveld *et al.* 2009). This northeastern lineage is the same as that identified as CmeB (Thiele *et al.* 2013) as part of the provisionally named *Cheirogaleus* sp. Bekaroka Sambava. Further field work in this diverse region is necessary to confidently describe this species.

5) UCS4: Known only from four individuals from one locality, Ambanja (Groeneveld *et al.* 2009). This northwestern lineage is the same as that identified as CmeC (Thiele *et al.* 2013) as part of the provisionally named *Cheirogaleus* sp. Ambanja. Further field work in this geographical area is recommended as it is bounded by the Mahavavy Nord and Sambirano rivers, which have been shown to be effective genetic barriers for the genus *Lepilemur* (Louis *et al.* 2006).

4. *C. sibreei* group

**External characters**: Eye-rings variable, usually grey-black, and less broadly connected to the dark grey muzzle than in *C. crossleyi* group. Ears dark but not black, thinly haired. Interorbital facial strip comparatively broad. Body and head medium grey, with strongly marked deep brown dorsal stripe, and tail tip darkened. Underside and inner aspect of limbs, and underside of basal part of the tail, white, sharply marked off from the color of upperside, and extending well up on the flanks and neck.

**Skull**: Facial skeleton short, low, slightly convex; orbits somewhat of *medius* type, but less marked; interorbital space narrow; inferior orbital margins not markedly anterior to the superior margins, so orbit looking fairly forward, its dorsal rim very slightly interrupting the dorsal outline of the skull; postorbital constriction not so marked; nasals well raised above the maxillae, even more so than in the *medius* group; rostrum straight-sided, then suddenly converging anteriorly; premaxillae suddenly and strongly converging to a point; lateral margin of the pyriform aperture strongly concave in lateral view; nasal tip very long. Braincase steeply descending posteriorly, but shorter than in the *major* group. Bullae large, protruding well below the alveolar line; temporal lines well expressed. Vomer not prolonged backward, basisphenoid not ridged, lateral pterygoid plates not flared; posterior palatal margin strongly concave; bullae greatly enlarged.

**Dentition**: Toothrows straight and converging forward until P2 level, when they run parallel until anterior to the canines; incisors not projecting; canines noticeably large, long and slender and with a distal cusp, like the *medius* group; P2 and especially P3 and P4 larger than the *major* group, but similar in shape; P3 somewhat raised, with diastema both mesial and distal to it; molar cusps high, upper molars very rounded lingually; M3 very triangular in form, its distolingual margin a simple straight edge.

***Cheirogaleus sibreei*** (Forsyth Major, 1896). *Ann. Mag. Nat. Hist.* 6th series 18: 325.

*Chirogale Sibreei* Forsyth Major, 1896

*Summary*: *Cheirogaleus sibreei* has been consistently supported as a monophyletic species (Groeneveld *et al.* 2009, 2010; Thiele *et al.* 2013), and does not currently require additional taxonomic work. This lineage would, however, benefit from further field studies. The type locality of *C. sibreei* is Ankeramadinika, but this name is no longer used. In Mrs. Standing's short essay from 1904 on her missionary work titled "The F.F.M.A. Sanatorium, Ankeramadinika, Madagascar," she mentions that this village was abandoned and clearly describes its location as being near Ambatolaona, which agrees with Forsyth Major's comment of being one day's journey east of Antananarivo. The first extant population of *C. sibreei* was recently documented south of Ankeramadinika in Tsinjoarivo and was sympatric with *C. crossleyi* (Blanco *et al.* 2009; Groeneveld *et al.* 2010). Not only are these species sympatric, they were documented occupying a single tree hole in Anjozorobe that had four individuals identified as *C. crossleyi* and one as *C. sibreei* (E. E. Louis Jr., pers. obs.).

*Type*: BM 97.9.1.160, skin and skull

*Type locality*: Ankeramadinika

*Distribution*: Along the central high plateau from Anjozorobe Protected Area in the north through Tsinjoarivo down to Ranomafana National Park in the south.

*Vernacular name*: Sibree's dwarf lemur.

***Cheirogaleus sibreei* group**: other potential species

1) *Cheirogaleus minusculus* Groves, 2000. *Int. J. Primatol*. 21: 960. This species seems closest to *C. sibreei*, with the same dorsal stripe, relatively restricted eye rings, a grey muzzle, and dark, thinly haired ears. The type is much smaller than *C. sibreei*, with a higher and more rounded braincase, the facial skeleton is not convex, the palate is broader, and the upper third molars very reduced; the tail tip appears to be white. *Cheirogaleus minusculus*, known only from the type locality of Ambositra (Groves 2000), is still Data Deficient and requires intensive field and laboratory investigation to confirm its taxonomic status.

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## Appendix I

(a). Appendix I(a). Phylogenetic relationships between *Cheirogaleus* species inferred from the maximum likelihood and Bayesian approaches of the complete COII sequence data (684 bp) generated from 134 individuals with four out-group taxa. New field samples were labeled in bold. Numbers on branches represent maximum likelihood values followed by posterior probability support. Tip labels include locality, followed by number of individuals carrying the haplotype in brackets, then the locality numbers.

(b). Appendix I(b). Phylogenetic relationships between *Cheirogaleus* species inferred from the maximum likelihood and Bayesian approaches of the partial vWF sequence data (792 bp) generated from 208 individuals with four out-group taxa. Sequences generated from new field samples were labeled in bold and published sequences derived from museum specimens were presented in italics. Numbers on branches represent maximum likelihood values followed by posterior probability support. Tip labels include locality, followed by number of individuals carrying the haplotype in brackets, then the locality numbers.

(c). Appendix I(c). Phylogenetic relationships between *Cheirogaleus* species inferred from the maximum likelihood and Bayesian approaches of the partial FIBA sequence data (606 bp) generated from 208 individuals with four out-group taxa. Sequences generated from new field samples were labeled in bold and published sequences derived from museum specimens were presented in italics. Numbers on branches represent maximum likelihood values followed by posterior probability support. Tip labels include locality, followed by number of individuals carrying the haplotype in brackets, then the locality numbers.

(d). Appendix I(d). Skulls of species in the genus *Cheirogaleus* used in morphometric comparisons.

## Appendix II

(a). Appendix II(a). Table S1 Sample localities of *Cheirogaleus.*

(b) Appendix II(b). Table S2 Cranial and dental (maxillary) measurements of *Cheirogaleus* taxa.

(c) Appendix II(c). Table S3 External metrics of *Cheirogaleus* taxa. HB = head+body length, HF = hindfoot length. Measurements from the literature of the types of *major*/*milli* and *typicus* are given for comparative purposes.

(d) Appendix II(d). Table S4 *Cheirogaleus* specimens deposited at the following institutions: American Museum of Natural History, New York (AMNH), Natural History Museum, London (BMNH), Field Museum of Natural History, Chicago (FMNH), Institut für Anthropologie, Johannes Gutenberg-Universität Mainz, Germany (IFA), Museum of Comparative Zoology, Harvard (MCZH), Muséum National d'Histoire Naturelle, Paris (MNHN), Museum für Naturkunde - Leibniz Institute for Evolution and Biodiversity Science (MfN/ZMB), and Naturalis Biodiversity Center (formerly Rijksmuseum van Naturlijk Historie – NMNL). Spelling of localities is consistent with records associated with specimens and does not necessarily correspond to modern spellings; latitude and longitude were estimated *post hoc* except for those at IFA. Specimens verified as *Cheirogaleus* were arranged by species and clade when possible and then by locality. An abbreviated history of determinations was included for examined specimens. Unverified specimens in italics refer to catalog numbers in institutional databases identified as *Cheirogaleus*, but were not confirmed by the authors.

(e). Appendix II(e). Table S5 Primers used in this study.

(f). Appendix II(f). Table S6 Accession numbers of published *Cheirogaleus* sequences from Genbank (NCBI).

(g). Appendix II(g). Table S7 Genetic distance matrix for mtDNA cytb sequence data between and within clades of *Cheirogaleus*.

(h). Appendix II(h). Table S8 Genetic distance matrix for mtDNA PAST fragment sequence data between and within clades of *Cheirogaleus*.

(i) Appendix II(i). Table S9 Genetic distance matrix for mtDNA D-loop sequence data between and within clades of *Cheirogaleus*.

(j) Appendix II(j). Table S10 Genetic distance matrix for mtDNA COII sequence data between and within clades of *Cheirogaleus*.

(k) Appendix II(k). Table S11 Genetic distance matrix for nucDNA CFTR-PAIRB sequence data between and within clades of *Cheirogaleus*.

(l) Appendix II(l). Table S12 Genetic distance matrix for nucDNA FIBA sequence data between and within clades of *Cheirogaleus*.

(m) Appendix II(m). Table S13 Genetic distance matrix for nucDNA VWF sequence data between and within clades of *Cheirogaleus*.

(n) Appendix II(n). Table S14 Diagnostic nucleotide sites from the mtDNA cytb Pairwise Aggregate Analysis (PAA) of *Cheirogaleus*. No.PAA stands for number of diagnostic nucleotide sites.

(o) Appendix II(o). Table S15 Diagnostic nucleotide sites from the mtDNA PAST fragment Population Aggregate Analysis (PAA) of *Cheirogaleus*. No.PAA stands for number of diagnostic nucleotide sites.

(p) Appendix II(p). Table S16 Diagnostic nucleotide sites from the mtDNA D-loop Population Aggregate Analysis (PAA) of *Cheirogaleus*. No.PAA stands for number of diagnostic nucleotide sites.

(q) Appendix II(q). Table S17 Diagnostic nucleotide sites from the mtDNA COII fragment Population Aggregate Analysis (PAA) of *Cheirogaleus*. No.PAA stands for number of diagnostic nucleotide sites.

(r) Appendix II(r). Table S18 Variable and diagnostic nucleotide sites (shaded) from the nucDNA CFTR-PairB Population Aggregate Analysis (PAA) of *Cheirogaleus*. No.PAA stands for number of diagnostic nucleotide sites.

(s) Appendix II(s). Table S19 Variable and diagnostic nucleotide sites (shaded) from the nucDNA FIBA Population Aggregate Analysis (PAA) of *Cheirogaleus*. No.PAA stands for number of diagnostic nucleotide sites.

(t) Appendix II(t). Table S20 Variable and diagnostic nucleotide sites (shaded) from the nucDNA vWF Population Aggregate Analysis (PAA) of *Cheirogaleus*. No.PAA stands for number of diagnostic nucleotide sites.

(u) Appendix II(u). Table S21 Morphometric data (mm) collected from sedated *Cheirogaleus* individuals. Clades were designated based on mtDNA sequence data (Figure 2). Morphological data is missing, HC: head crown, BL: Body Length, TL: Tail Length, F-Tb: Front Thumb (forelimb), F-UR: Front Ulna/radius, F-Hd: Front Hand, F-LD: front longest digit (Forelimb), F-H: Front Humerus, H-T: Hind Tibia, H-LD: hind longest digit (Hindlimb), H-Ft: Hind foot, H-Tb: Hind Thumb (Hindlimb). H-F: Hind Femur, UC: Upper Canine, LC: Lower Canine, RTL: Right Testes Length, RTW: Right Testes Width, LTL: Left Testes Length, LTW: Left Testes Width.

*Primate Conservation* 2014 (28): 37–38

# Announcing the Lemur Conservation Network

## *Working Together to Save Lemurs from Extinction*

LEMUR
CONSERVATION NETWORK
www.lemurconservationnetwork.org

The Lemur Conservation Network is scheduled to launch in early 2015 at <www.lemurconservationnetwork.org>. This website will unite organizations that are working to save Madagascar's lemurs from extinction with people who want to join and support the cause. It will serve as a funding guide for individuals and potential donors who want to support lemur conservation and the *IUCN Lemur Action Plan*[1], and as a resource for organizations who want to promote their work in lemur conservation.

Each participating organization will have a page on the site to share their story with donors, so that individuals can get to know the variety of organizations working to save Madagascar's unique wildlife, and find organizations to support. The site will link to each organization's donation page to encourage immediate action from site visitors.

The Lemur Conservation Network aims to be a site that people will want to visit again and again. Our blog will feature posts from a variety of researchers and conservation leaders, so potential donors can learn about conservation on the ground in Madagascar, and become even more interested in preserving Madagascar's natural wonders. Our Facebook page will engage lemur fans worldwide and drive them to the website for donations.

It is free for organizations to participate! The Lemur Conservation Network does not take a portion of donations or charge for participation. If your organization would like to be included or you are interested in writing a blog post, please email Kim Reuter, Director of Outreach and Content, at <kimeleanorreuter@gmail.com>.

The Lemur Conservation Network is a project of the Madagascar Section of the IUCN SSC Primate Specialist Group, with support from lemur conservationists Christoph Schwitzer, Steig Johnson, Jonah Ratsimbazafy and Kim Reuter. Marketing and web design services have been donated by Lynne Venart of The Art Monkey LLC, and the web hosting support was donated by the Bristol Zoological Society.

*We are stronger together. Let's work together to save lemurs from extinction.*

Join us at <www.lemurconservationnetwork.org>. Find us on Facebook at: <www.facebook.com/lemurconservationnetwork>.

**Kim Reuter**, Director of Outreach and Content. E-mail: <kimeleanorreuter@gmail.com>
**Lynne Venart**, Project Manager & Creative Director, Lemur Conservation Network

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[1] Schwitzer, C., R. A. Mittermeier, N. Davies, S. Johnson, J. Ratsimbazafy, J. Razafindramanana, E. E. Louis Jr. and S. Rajaobelina (eds.). 2013. *Lemurs of Madagascar: A Strategy for their Conservation 2013–2016*. IUCN SSC Primate Specialist Group, Bristol Conservation and Science Foundation, and Conservation International, Bristol, UK, and Arlington, VA. 185pp. Website: <http://www.primate-sg.org/storage/pdf/Lemurs_of_Madagascar_Strategy_for_Their_Conservation_20132016_low_res.pdf>.

Dancing Verreaux's sifaka (*Propithecus verreauxi*), Berenty, Madagascar, October 2005. Photo by Russell A. Mittermeier ©Conservation International.

Goodman's mouse lemur (*Microcebus lehilahytsara*), Andasibe, Madagascar, March 2007. Photo by Russell A. Mittermeier ©Conservation International.

Male and female rufous-fronted brown lemur (*Eulemur rufifrons*). Camping site on trail to Cascade des Nymphes, Isalo National Park, Madagascar. Photo by Russell A. Mittermeier ©Conservation International.

*Primate Conservation* 2014 (28): 39–42

# Special Section on the Crowned Sifaka *Propithecus coronatus*: Introduction

Guest editors: Josia Razafindramanana[1], Tony King[2], Lounès Chikhi[3], Christoph Schwitzer[4] and Jonah Ratsimbazafy[1]

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Madagascar is home to over 100 endemic lemur taxa (Schwitzer *et al.* 2013), one of which is the crowned sifaka *Propithecus coronatus*. As with the vast majority of lemurs (a staggering 94% according to Schwitzer *et al.* 2013), the crowned sifaka is threatened with extinction; it is currently ranked as Endangered on the IUCN Red List (Andriaholinirina *et al.* 2014). In February 2011, following the discovery of several small and isolated populations distributed across central Madagascar (Razafindramanana and Rasamimanana 2010; King *et al.* 2012; Rakotonirina *et al.* 2014), a number of stakeholders, including government ministries and non-governmental organizations, participated in a workshop with the aim of sharing and updating information on the crowned sifaka, and of discussing conservation approaches for such fragmented populations (MEF/GERP/TAF 2011). This special section of *Primate Conservation*, focusing on the crowned sifaka, is one outcome of that workshop.

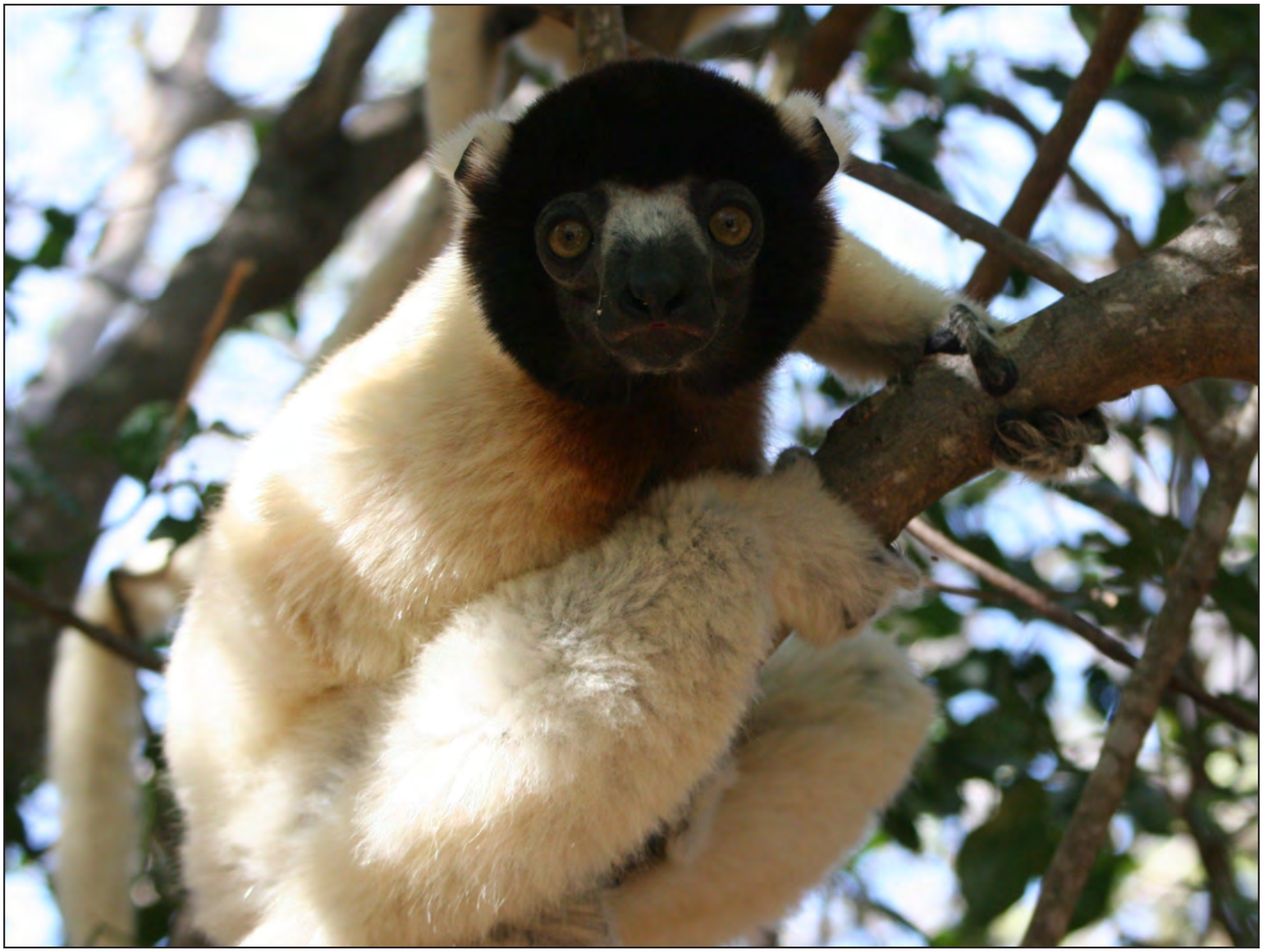
The special section has taken much longer to publish than we had originally hoped, for which we apologize. One reason is related to the usual issues of authors finding the time to write, submit and revise their papers, and of reviewers and editors finding the time to review and edit. Another, more interesting reason is that during the review and editing process of virtually every paper, it became increasingly clear that the crowned sifaka is a remarkably little-known and misunderstood primate. The need to publish this special section has therefore become ever more pressing, and we hope that the papers presented herein will clarify many issues regarding the species, and also highlight others which remain in dire need of investigation and resolution.

The distribution of the crowned sifaka in the wild, which has often been erroneously described in recent years despite fairly accurate descriptions provided by early explorers such as Milne-Edwards and Grandidier (1875), is described, refined, and described again, by Rakotonirina *et al.* (2014) and King *et al.* (2014), based on a series of field surveys and a comprehensive literature review. These two papers also describe in detail the chromatic variation observed in crowned sifaka and the closely related Decken's sifaka *Propithecus deckenii*, providing maps illustrating the distribution of chromatically variable populations of the two taxa. The authors argue that, although individuals resembling both taxa may sometimes be found in sympatry, and chromatically variable populations may be the result of gene-flow between them, there is no evidence of the occurrence of sympatric populations of the two taxa, as has been suggested in the past. The two papers also summarize the taxonomic uncertainties surrounding the validity of the specific status of the crowned sifaka.

The abundance of the crowned sifaka in the northern part of its distribution is presented by Salmona *et al.* (2014), based on an extensive series of transect surveys. These authors extrapolate their density estimates across the entire range of the crowned sifaka, to give an indication of total population size, and propose an updated conservation assessment of the species based on the IUCN Red List criteria.

The paper by Andriamasimanana and Cameron (2014) provides a quantitative assessment of changes over time of the habitat available to crowned and Decken's sifakas within one of the largest protected areas in their range, the Mahavavy-Kinkony wetland complex. Habitat loss and fragmentation are considered as two of the major causes of past and predicted population decline in the crowned sifaka, so this paper provides valuable insights into the dynamics of habitat change in this region.

By far the best-studied population of crowned sifaka occurs in the far north of its range, in the Antrema Forest Station. A long-term research and conservation project has been ongoing there since 1998 (Gauthier *et al.* 1999; Pichon *et al.* 2010). The paper by Ramanamisata *et al.* (2014) provides further information on this population, presenting the results of their study on the social behavior and dominance hierarchy in three groups of crowned sifaka. The authors report that the most frequently observed social behaviors were, in descending order, allogrooming, agonistic behaviours, and play. They ascertained a social hierarchy, with



The crowned sifaka, *Propithecus coronatus*, Katsepy, Madagascar, July 2010. Photo by Tony King / The Aspinall Foundation.

females dominating males, and found that, although groups defended their territories, the most frequent outcome of intergroup interactions was tolerance.

Antrema was also the site chosen by Fichtel (2014) for her study of the acoustic structure of the loud calls ("tchi-faks") of crowned sifakas, which she compared with the calls of Decken's sifakas at Bemaraha, finding that the calls differed significantly between the two populations. Fichtel also found that the "tchi-faks" of both populations were highly individually distinctive. The study highlights several interesting hypotheses, the verification of which will require study of additional populations of the two species.

Finally, Roullet (2014) provides a thorough overview of the small captive population of crowned sifaka, presenting the results and lessons learnt during 25 years of captive management since the first export from Madagascar to Paris in 1987. Roullet concludes her article with a summary of the support that European holders of crowned sifaka provide to the conservation of the species in Madagascar. This includes the initiation of the project at Antrema by the Parc Zoologique de Paris (Muséum national d'histoire naturelle), the creation and coordination of the Tsibahaka Project by The Aspinall Foundation, and the facilitation and support by several European organizations of a metapopulation management approach to integrating *ex situ* and *in situ* conservation of the crowned sifaka. This latter is implemented under the Sifaka Conservation Project, in close collaboration with European institutions and GERP (*Groupe d'Etude et de Recherche sur les Primates de Madagascar*). Several of the small or isolated populations of crowned sifaka newly reported from central Madagascar by Razafindramanana and Rasamimanana (2010), King *et al.* (2012) and Rakotonirina *et al.* (2014) have subsequently benefited from community-based conservation interventions within the framework of the metapopulation conservation project.

The collection of papers presented in this special section gives a good overview of the current state of our knowledge about the conservation needs and ecology of the crowned sifaka. Conservation action plans for several sites with crowned sifaka populations have recently been described (Rakotonirina *et al.* 2013; Ramanamisata and Razafindraibe 2013; Razafindramanana *et al.*

2013a, 2013b), but support and funding for these and other priority sites for the species is still required. Clearly there is still much to be learnt, and much to be done, to ensure the continued survival of this remarkable primate across the entirety of its range.

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

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**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

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## 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 *P. coronatus*** | | | | | | | |
| Boeny | Ambato Boeny | Anaboazo | 4 groups; also 2 groups of *Eulemur mongoz* | 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 *Eulemur rufus* | 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 *P. deckeni* 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 | Ambalanjanakomby | Betonendry / Maroakanga | *P. coquereli* | 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 | Tsaratanàna | Sifaka apparently absent | Aug | 19.281°S 45.718°E | 800-989 | LR, FR |
| Amoron'i Mania | Mangataboahangy | Andakata - Ambolokely | *P. verreauxi* | Dec | 20.339°S 46.237°E | 852-855 | RR, AR |
| Amoron'i Mania | Amborompotsy | Andondona: Analakinganala | *P. verreauxi* | Jan | 20.534°S 46.347°E | 1338-1339 | RR, AR |

[a] Observers: LR: Laingoniaina Rakotonirina; FR: Fetraharimalala 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 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).

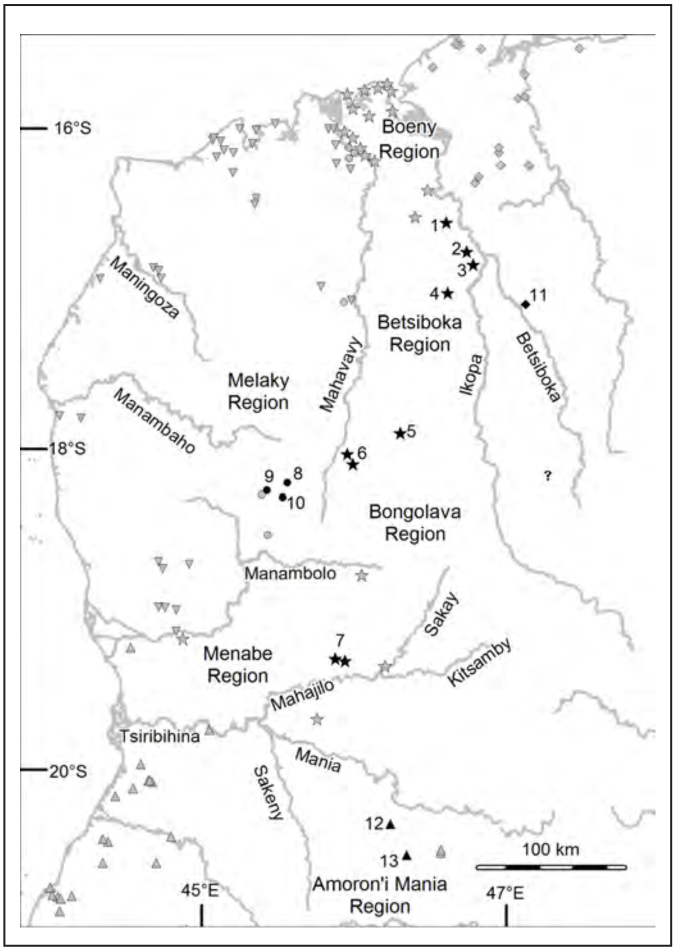

**Figure 1.** Map of west and western central Madagascar showing distributional records of four sifaka species in relation to regions and major rivers. New sites reported here are given as numbered black symbols, and previously published sites as grey symbols, of *P. coronatus* (stars), *P. deckenii* (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 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 *P. coronatus*** | | | | | | | | |
| 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 |
| Mahajeby | Andafy atsinanan'ny Tongopapango 2 | 05/03/2010 | 18.095°S | 45.993°E | 679 | 4 | 0 | 0 |
| Mahajeby | 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 *P. deckenii* 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 (*P. deckenii*) | 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** | **Antsakatsarotra** | **Orimbato** |
|---|---|---|---|---|---|---|---|---|---|---|
| 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 | ? | Protection | 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 Anaboazo 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 Ikay 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 Ikay site is 60 km southeast 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*.

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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.

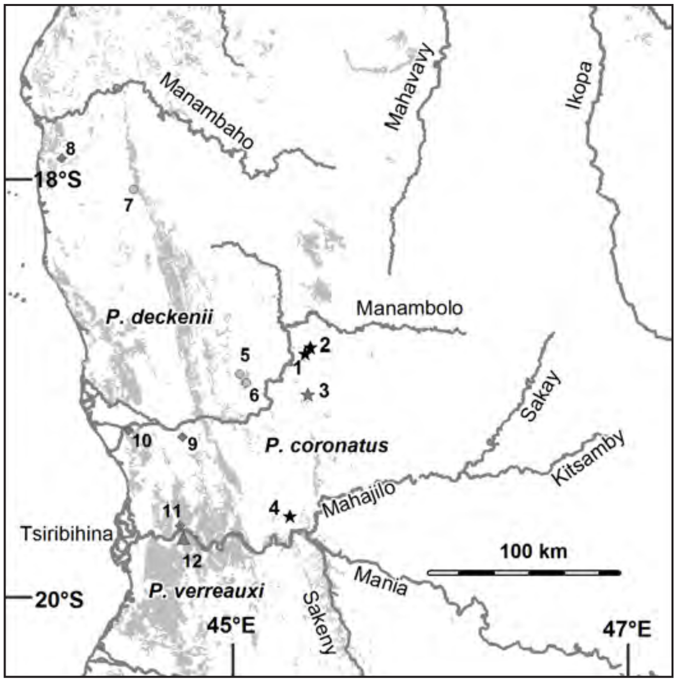

**Figure 1.** Map of the study site in western Madagascar showing major rivers (dark gray), approximate forest cover (light gray), and survey sites (numbered symbols) where we observed typical *P. coronatus* only (gray stars), *P. coronatus* occurring with melanistic forms (black stars), *P. deckenii* (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

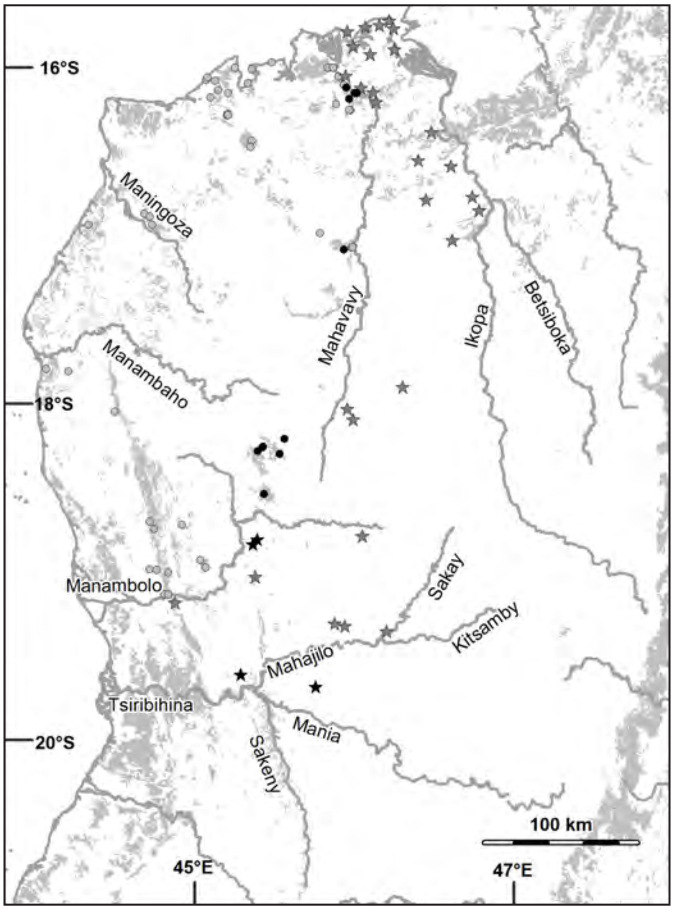

**Figure 2.** Map of west and western central Madagascar showing major rivers (dark gray), approximate forest cover (light gray), distributional records of *P. coronatus* (gray stars), *P. deckenii* (gray circles), *P. coronatus* occurring sympatrically with melanistic forms (black stars) and *P. deckenii* 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 |

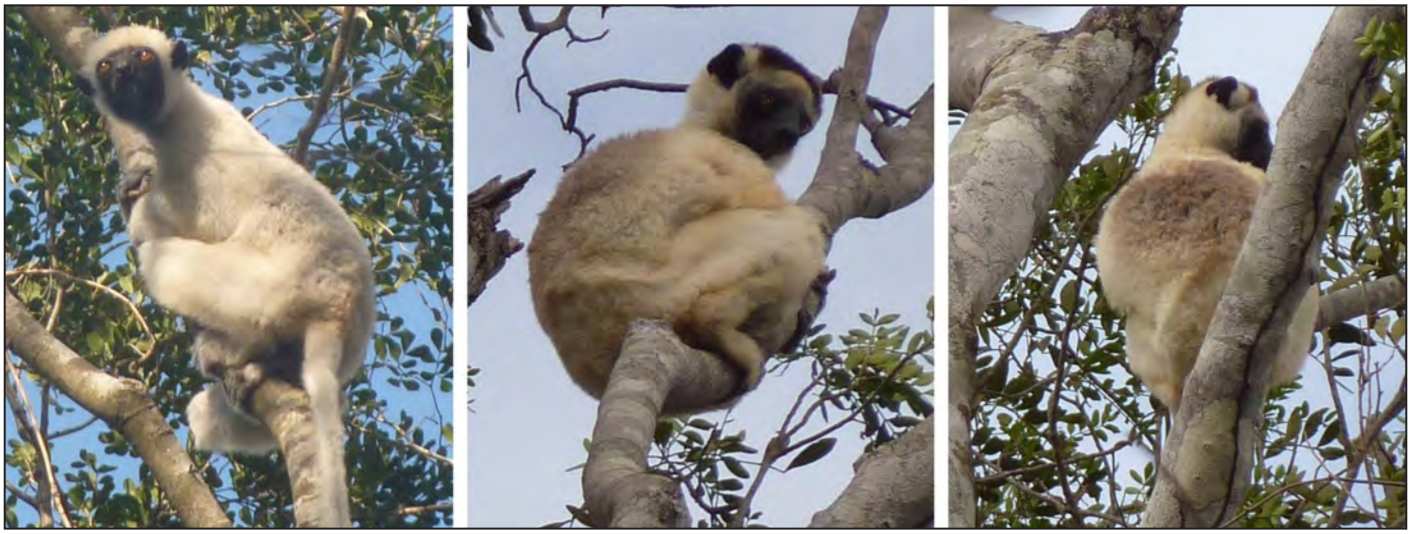

**Figure 3.** A typical *P. deckenii* at the Bevinoa survey site (left), and a *P. verreauxi* showing a fairly dark back at the Ambalakapoaky survey site. Photographs by L. Rakotonirina.

**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.

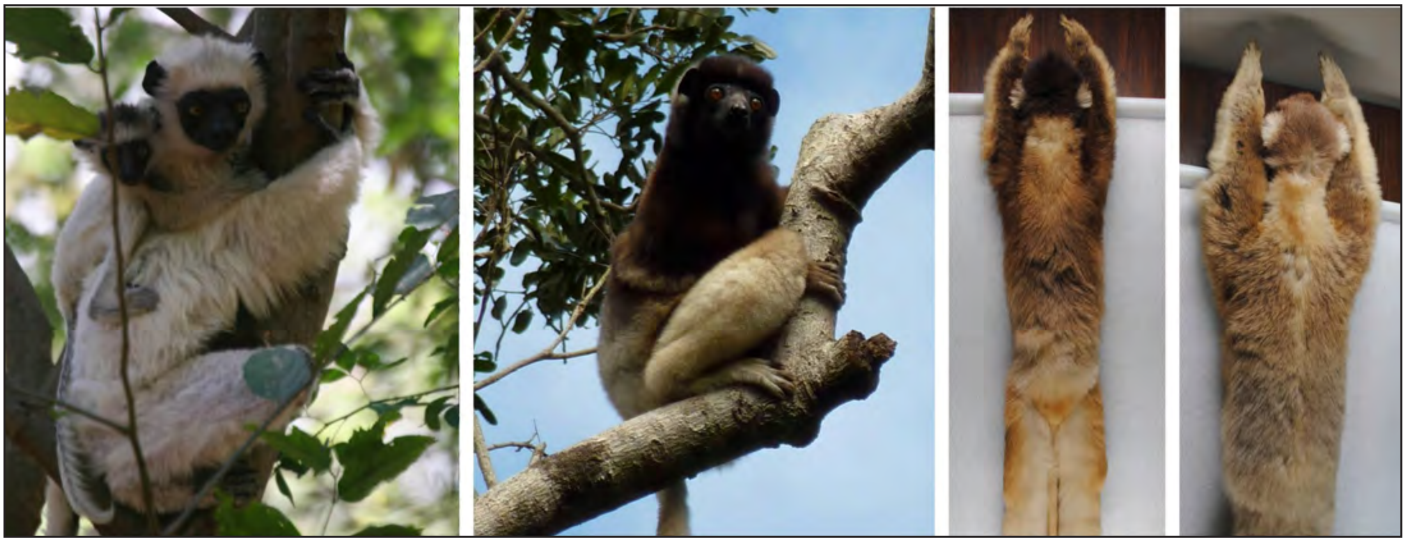

**Figure 8.** A pale form of *P. verreauxi* with a white rather than brown cap at Berenty private reserve, southern Madagascar, in October 2010 (left); a melanistic form of *P. deckenii* at Orimbato, near Ambohijanahary Special Reserve, in March 2010 (center; see Rakotonirina *et al.* 2014), and two 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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# Spatio-temporal Change in Crowned (*Propithecus coronatus*) and Decken's Sifaka (*Propithecus deckenii*) Habitat in the Mahavavy-Kinkony Wetland Complex, Madagascar

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**Abstract:** The crowned sifaka (*Propithecus coronatus*) and Decken's sifaka (*Propithecus deckenii*) are Endangered lemurs endemic to west and central Madagascar. Both have suffered habitat loss and fragmentation throughout their ranges. The goal of this study, conducted in the Mahavavy-Kinkony Wetland Complex (MKWC) in northwestern Madagascar, was to assess the effects of historical change in the species' habitats, and to model the potential impact of further land-use change on their habitats. The IDRISI Andes Geographical Information System and image-processing software was used for satellite-image classification, and the Land Change Modeler was used to compare the natural habitat of the species from 1973 to 2005, and to predict available habitat for 2050. We analyzed two forests in the MKWC occupied by *P. coronatus* (Antsilaiza and Anjohibe), and three forests occupied by *P. deckenii* (Tsiombikibo, Marofandroboka and Andohaomby). The two forests occupied by *P. coronatus* contracted during the period 1949–1973, but then expanded to exceed their 1949 area by 28% in 2005. However, the land change model predicted that they will contract again to match their 1949 area by 2050, and will again lose their corridor connection, meaning that the conservation gains for this species in the complex are at risk of being reversed. The three forests occupied by *P. deckenii* have declined in area steadily since 1949, losing 20% of their original area by 2005, and are predicted to lose a further 15% of their original area by 2050. Both species are therefore at risk of becoming even more threatened if land-use change continues within the complex. Improved conservation of the remaining forest is recommended to avoid further loss, as well as ecological restoration and reforestation to promote connectivity between the forests. A new strategy for controlling agriculture and forest use is required in order to avoid further destruction of the forest.

**Key Words:** *Propithecus coronatus*, *Propithecus deckenii*, threats, deforestation, fragmentation, prediction, conservation

## Introduction

Sifakas (*Propithecus*) are endemic to Madagascar. Of the nine species currently recognized (Mittermeier *et al.* 2010), four are classified on the IUCN Red List as Critically Endangered, and five, including the crowned sifaka (*P. coronatus*) and Decken's sifaka (*P. deckenii*), as Endangered (Andriaholinirina *et al.* 2014a, 2014b). Crowned and Decken's sifaka are found in dry deciduous forest in west and central Madagascar. In the north of its range, the crowned sifaka is found between the Mahavavy and Betsiboka rivers, and recent surveys have shown that its full distribution extends southwards through the fragmented forests of the Boeny, Betsiboka, Bongolava and Menabe regions towards the rivers Tsiribihina, Mahajilo, and Mania (King *et al.* 2012, 2014; Rakotonirina *et al.* 2014; Salmona *et al.* 2014). Decken's sifaka is found to the west of the Mahavavy River, its distribution extending south to the Manambolo River (Mittermeier *et al.* 2010; King *et al.* 2014). Sifaka color variations occur towards the lower reaches of the Mahavavy and Manombolo rivers, at sites in the Melaky and Menabe Regions, with melanistic forms reported in populations of both crowned and Decken's sifakas (King *et al.* 2014; Rakotonirina *et al.* 2014). Similar color variations have also been reported in populations of Decken's sifaka further north, including that of the Mahavavy-Kinkony Wetland Complex (Curtis *et al.* 1998; Thalmann *et al.* 2002; Rumpler *et al.* 2011; Rakotonirina *et al.* 2014).

Three new protected areas in western Madagascar will help conserve the crowned sifaka; the Mahavavy-Kinkony Wetland Complex (MKWC), Bombetoka-Belemboka, and the forest station of Antrema, with the MKWC providing approximately two-thirds of the protected area occupied by this species (Rasoavahiny *et al.* 2008). Decken's sifaka is also present in the MKWC and several other protected areas, including three national parks (Mittermeier *et al.* 2010). The

MKWC is, therefore, important for the conservation of these two sifaka species.

Habitat destruction, degradation and fragmentation are the principle drivers of population declines of both crowned and Decken's sifakas (Andriaholinirina *et al.* 2014a, 2014b). Historical changes in forest habitat are due to various factors, among which anthropogenic factors are the primary contributors (ZICOMA 1999; McConnell 2002). This research was undertaken in the MKWC in order to analyze the direction and rate of change of the natural habitat of crowned and Decken's sifakas to inform conservation strategies for their survival within the site.

## Study Site

The Mahavavy-Kinkony Wetland Complex (MKWC) is located in the Boeny Region of northwest Madagascar (45°28' to 45°56'E, 15°46' to 16°12'S) at low elevations up to 150 m above sea level (ZICOMA 1999; Andriamasimanana and Rabarimanana 2011). The complex extends across 275,000 ha (Razafindramanana *et al.* 2013) to 300,000 ha (Andriamasimanana *et al.* 2013), incorporating the Mahavavy River delta, the Kinkony Lake, Marambitsy Bay, and several dry, deciduous forest fragments (BirdLife International 2014). The site is an Important Bird and Biodiversity Area (BirdLife International 2014); all the wetland bird species of western Madagascar have been recorded there. Threatened lemurs in the MKWC (Müller *et al.* 2000; Razafindramanana *et al.* 2013) include crowned and Decken's sifakas, mongoose lemur (*Eulemur mongoz*), and rufous brown lemur (*Eulemur rufus*).

A supervised classification of Landsat satellite images of the region from 2005 was conducted by Andriamasimanana *et al.* (2013) using the IDRISI Andes Geographical Information System and image processing software to define the major forms of land use in the complex (Fig. 1). Andriamasimanana *et al.* (2013) found that dry forest—the primary habitat for lemurs in the MKWC—dominated more than one-third (37%) of the complex (Table 1). This is followed by savannah, which covers a quarter (26%) of the surface area, whilst over one-fifth of the surface is occupied by wetland (18%) and mangrove (4%). The remainder of the complex consists of sand (7%), cultivated areas (7%), and salt marsh (1%).

Based on occurrence data for 19 threatened taxa (nine birds, three lemurs, three fishes, three bats and one reptile), Andriamasimanana *et al.* (2013) identified eight priority sites for biodiversity conservation in the MKWC. The eight priority sites included the reed marshes of Lake Kinkony, two mangrove areas, and five forest fragments (Andriamasimanana *et al.* 2013).

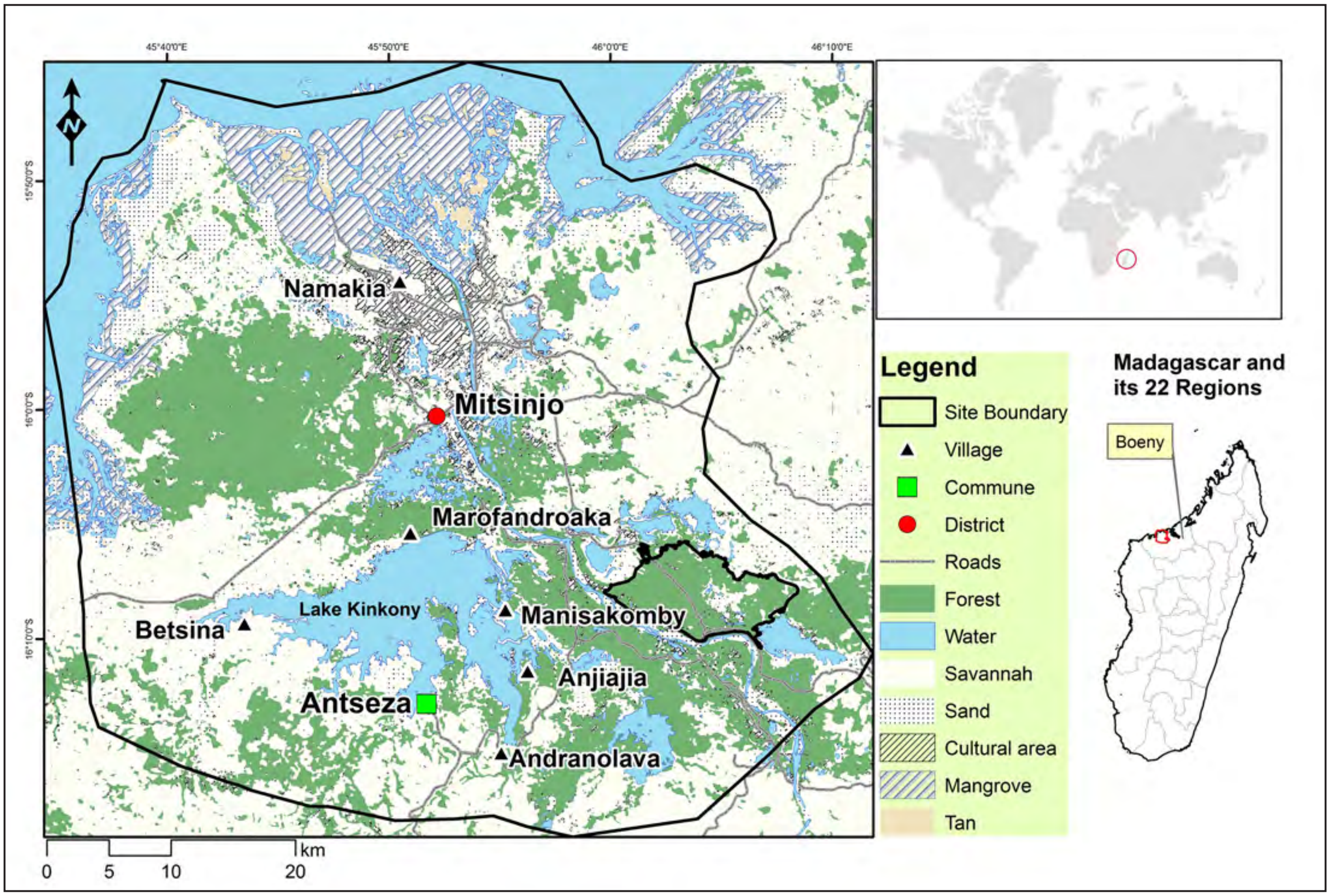

**Figure 1.** Map of the Mahavavy-Kinkony Wetland Complex and its main land-use classes in 2005.

**Table 1.** The seven main classes of land use of the Mahavavy-Kinkony Wetland Complex from the supervised classification of satellite images from 2005, following Andriamasimanana *et al.* (2013).

| Classes | Area(ha) | Land cover (%) |
|---|---|---|
| Dry forest | 111,559 | 37% |
| Savannah | 76,533 | 26% |
| Water | 54,860 | 18% |
| Cultivated area | 21,774 | 7% |
| Sand | 215,822 | 7% |
| Mangrove | 10,885 | 4% |
| Salt marsh | 1,863 | 1% |
| Total | 299,056 | |

## Methods

In this paper we considered the five priority forest fragments identified by Andriamasimanana *et al.* (2013) for analysis with respect to sifaka populations, although sifaka are known to occur in several other, mostly smaller, forest fragments in the MKWC (Curtis *et al.* 1998; Salmona *et al.* 2014). Crowned sifakas occur in the two study forests located to the east of the Mahavavy River (Antsilaiza and Anjohibe), and Decken's sifakas occur in the three study forests to the west (Tsiombikibo, Marofandroboka and Andohaomby); melanistic sifaka are found in the forests along the western bank of the Mahavavy River (Curtis *et al.* 1998; Thalmann *et al.* 2002; Rumpler *et al.* 2011; Rakotonirina *et al.* 2014), especially in the Andohaomby fragment.

We evaluated changes in forest cover from 1949 to 2005 for the five forest fragments by comparing the remote sensing results from 2005 with previous Landsat satellite images from 1973 and 1995, classified by Andriamasimanana *et al.* (2013), and with digitized topographic maps of the region from 1949, from Foibe Taosaritanin'i Madagasikarain (Andriamasimanana *et al.* 2013).

We then explored future changes in habitat in the five study forests by making a map of predicted forest cover in 2050 using the Land Change Modeler module in Idrisi Andes (Andriamasimanana *et al.* 2013). The first step consisted of developing potential transition maps from historical land-use changes through its integrated Neural network algorithm (Bhadeshia 1999). We used the Landsat satellite images from 1973, 1995, and 2005 for this model. The 1949 map was excluded because it was from a different source. The choice of factors used to create the potential transition maps was dictated by an understanding of the causes of change on the ground. Changes are largely driven by traditional agriculture, locally called *hatsaky*. This kind of agriculture needs previously forested land, near to water, easily accessed, and not far from the villages where the farmers live. Six factors were used to model the potential habitat transitions between 1973, 1995, and 2005. Two static factors (that do not change over time) were distance from rivers and slope. Four dynamic factors (that do change over time) were residential areas, roads including trails, the human population by *fokontany* (an administrative subdivision unit in Madagascar), and changes in the area of forest. This last dynamic factor was included in order to capture all other factors that could cause local changes, but which could not be identified from the literature and field surveys.

In order to test the ability of the land use change model to predict past habitat change, a performance test (Area Under the Receiver Operator Curve index; Fielding and Bell 1997) was undertaken using the result of the model of land-use change for 2005 (built from the 1973 to 1995 maps), and the classification of the 2005 Landsat image.

The second step was to run the land-use change model forward to make a prediction for the future; once the prediction was judged to be of high performance, the same parameters were kept and the model was projected forward to 2050. Future habitat vulnerability was determined by overlapping the predicted forest map for 2050 with the forest map of 2005. The areas that were covered only by 2005 forest were assumed to be vulnerable to change. As the analysis of habitat vulnerability is based on the land-use change model, the underlying assumptions are the same as those in the model: that there are no changes in conservation actions and that the existing pressures will continue into the future.

## Results

The Area Under the Receiver Operator Characteristic curve value that resulted from the validation test between the result of the land use change model for 2005 and the Landsat image classification for 2005 was 0.87, which is indicative of high performance (Pontius *et al*. 2000; Fielding and Bell 1997). Our spatial analysis showed that the three study forests occupied by Decken's sifaka—Andohaomby, Tsiombikibo and Marofandroboka—have suffered from continual deforestation from 1949 to 2005, each decreasing in size by 20%, 16% and 41%, respectively, and losing a total of 20% between them (Table 2). The land change model for 2050 predicts that

**Table 2.** Forest change between 1949 and 2005 and, predicted, between 2005 and 2050.

| Forest | Forest area in hectares | | | | | Area change (%) | | Sifaka[1] |
|---|---|---|---|---|---|---|---|---|
| | 1949 | 1973 | 1995 | 2005 | 2050 | 1949–2005 | 2005–2050 | |
| Anjohibe | 287 | 302 | 586 | 757 | 699 | 164% | –8% | Crowned |
| Antsilaiza | 2,373 | 1,172 | 1,870 | 2,646 | 1,968 | 11% | –26% | Crowned |
| Andohaomby | 9,743 | 7,661 | 8,785 | 7,751 | 4,325 | –20% | –44% | Decken's |
| Tsiombokibo | 27,960 | 25,705 | 22,745 | 23,490 | 20,730 | –16% | –12% | Decken's |
| Marofandroboka | 5,800 | 4,160 | 5,177 | 3,430 | 3,170 | –41% | –8% | Decken's |

[1] Melanistic sifaka occur in some forests in the MKWC; see text.

Decken's sifaka may lose a further 15% of its 1949 habitat in the MKWC by 2050 (Table 2; Figs. 2 and 3).

The two study forests occupied by the crowned sifaka contracted from 1949 to 1973, but then expanded to exceed their 1949 area by 28% in 2005 (Table 2; Fig. 3). The land-use change model predicts, however, that they will contract again to match their 1949 area by 2050 (Fig. 2 and 3). Further to this, the model predicts that the connecting corridor that formed between the two forests from 1949 to 2005 will be lost again by 2050 (Fig. 2).

## Discussion

Although interpretation of the Area Under the Receiver Operator Characteristic curve is rather subjective, the high value (0.87) falls within the range that is widely accepted as

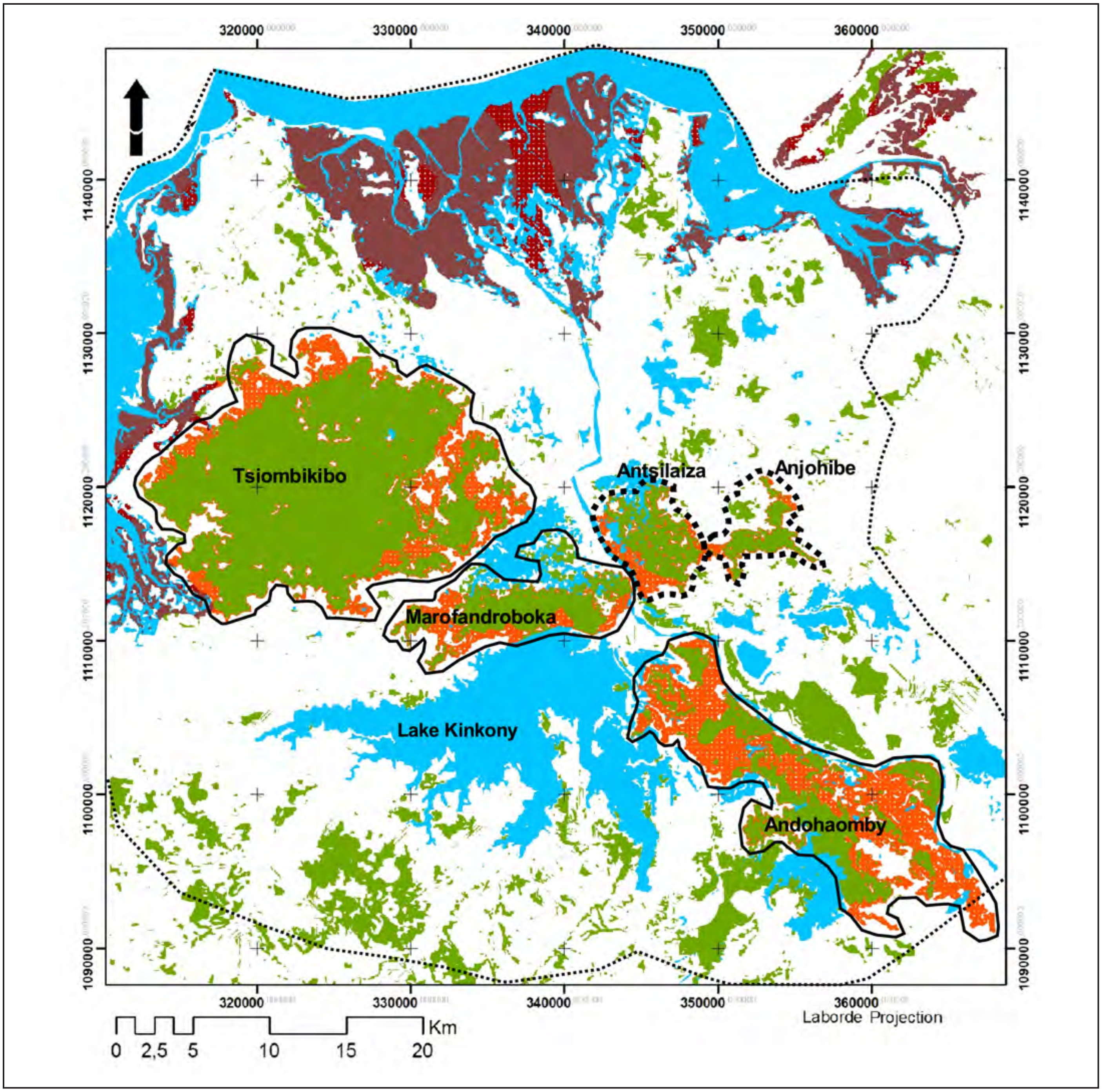

**Figure 2.** Prediction of habitat vulnerability in 2050 of the crowned sifaka (*Propithecus coronatus*) and Decken's sifaka (*Propithecus deckenii*) in the five study forests in the Mahavavy-Kinkony Wetland Complex. Vulnerable forest (orange) and remaining forest (green) are shown in the study forests occupied by crowned sifaka (within the heavy dotted lines) and those occupied by Decken's sifaka (solid lines). Other habitats include water (blue), remaining mangrove (purple) and vulnerable mangrove (red).

"excellent" (Pontius *et al*. 2000; Fielding and Bell 1997), indicating that the land-use change model is relatively robust and informative. While the results of the analysis of past habitat change are likely very robust because they rely on real data, it should be remembered that the modelled habitat change for 2050 is based on an assumption of "business as usual"—there will be no change (a) in conservation action, (b) in the ways in which the local population use their land for agriculture, (c) in mineral extraction, and (d) in external factors such as international economic pressures. The intention of providing this business-as-usual scenario is to inform the conservation strategy for the two sifaka species in the MKWC, providing the means to avoid any dire future that the model may predict.

Of the five forests analyzed in our study, the two located to the east of the Mahavavy River (habitat for crowned sifaka) increased in size between 1949 and 2005, while the three to the west (habitat for Decken's sifaka) shrank. The Anjohibe forest, the smallest of the study forests occupied by crowned sifaka, underwent a considerable increase in size of 164%; from 287 ha in 1949 to 757 ha in 2005. This increase is related to the geological structure on which this forest is located, and the fact that it is far from towns such as Mitsinjo and Namakia. The Anjohibe forest sits on a limestone formation (Du Puy and Moat 1997) that is unfavorable for agriculture. The Antsilaiza forest, the second supporting crowned sifaka, also lies on a limestone formation (Du Puy and Moat 1997). It also increased in size, but by less—12% between 1949 and 2005—due to it being closer to Mitsinjo. The future land-change model indicated that, as pressure for agricultural land increases, and if no interventions are planned, it is likely that, despite their marginal agricultural value and historical increase in size, both Anjohibe and Antsilaiza will shrink substantially to the extent that their combined area in 2050 might equal that of 1949 (Table 2).

Tsiombikibo is the largest forest in the MKWC. Of the three study forests that support Decken's sifaka, Tsiombikibo had shrunk the least since 1949 (16%). It is, however, threatened with a further reduction of 10% of its 1949 area by 2050. This 26%-loss represents a substantial reduction in the core population for this species in the MKWC. The Andohaomby forest lost a moderate percentage of 20% of its area between 1949 and 2005. It is located on an alluvial plain (Du Puy and Moat 1997) next to the Mahavavy River where silt from flooding replenishes the soil every summer. Its high agricultural potential is offset by its remoteness, being a long way from Mitsinjo and Namakia. The model indicates a future loss, however, of a further 36%, reducing its size to 44% of its area in 1949. Marofandroboka has suffered the largest historical loss of its forest; 41% since 1949. The model predicts, however, that its rate of loss may slow in future, and that it is likely to lose only a further 4% over the next 45 years, with 55% of its 1949 area remaining in 2050.

Lacking measures to reduce human pressure on the forests of the MKWC, the conservation gains benefiting the crowned sifaka in terms of increases in habitat area and connectivity since 1949 are at risk of being reversed, and the population is likely to decline to its 1949 level (Fig. 3). As crowned sifaka populations are also declining outside of protected areas (King *et al.* 2012; Andriaholinirina *et al.* 2014a), the species will be increasingly threatened unless measures can be taken to promote a recovery of its numbers in protected areas. The corridor that has grown between the Antsilaiza and Anjohibe forests since 1949 helps to maintain vital metapopulation processes. The fragmentation of this population if the corridor is once again lost will be particularly damaging for this large and highly forest-dependent species (Andriamasimanana *et al.* 2001).

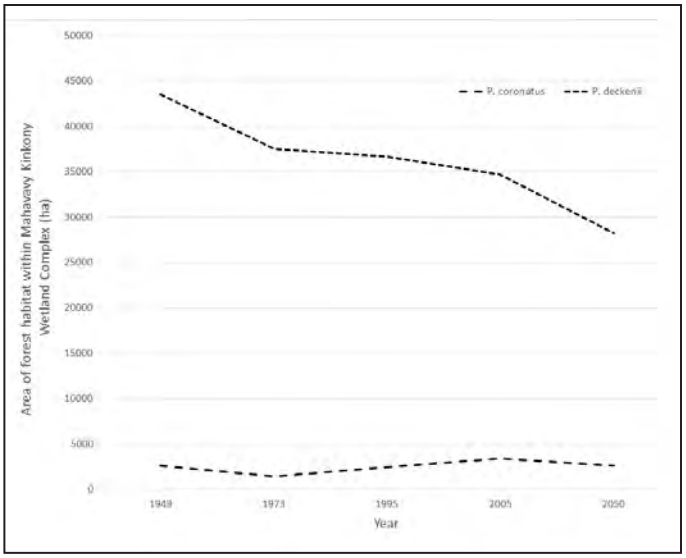

**Figure 3.** Habitat available for crowned and Decken's sifaka in the five study forests in the Mahavavy-Kinkony Wetland Complex from 1949 to 2050.

The outlook for Decken's sifaka under our business-as-usual model of land-use change is likewise not positive. The areas of the three study forests occupied by Decken's sifaka have declined steadily since 1949 (Table 2), shrinking 20% overall by 2005 (Fig. 3). The model predicts the loss of a further 15% with an increase in fragmentation by 2050 (Fig. 1). Although the total habitat for Decken's sifaka is currently much larger than that for the crowned sifaka (Fig. 3), the population will also decline, compromising its viability, if forest loss in the MKWC is allowed to continue.

A reduction in human pressure on the forests of the Mahavavy Kinkony Wetland Complex will be critical for the conservation of these two sifakas. An important measure for the Andohaomby forest will be the creation of a path, usable during the dry season, to provide access to and allow people to travel through the forest. If access to the forests is restricted then it is essential that measures be put in place to increase the production capacity of the local farmers, promoting a cost-effective agriculture that eliminates the need for deforestation and the destructive collection of firewood. Reforestation is necessary throughout the MKWC to maintain and restore connectivity and the ecological functions of the sifaka's habitats.

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

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**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 $km^2$), 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 Andriatsarafara 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 Tsiroanomandidy, south of the Manambolo River (in Wilmé *et al*. 2006). Later, Petter and Andriatsafara (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.

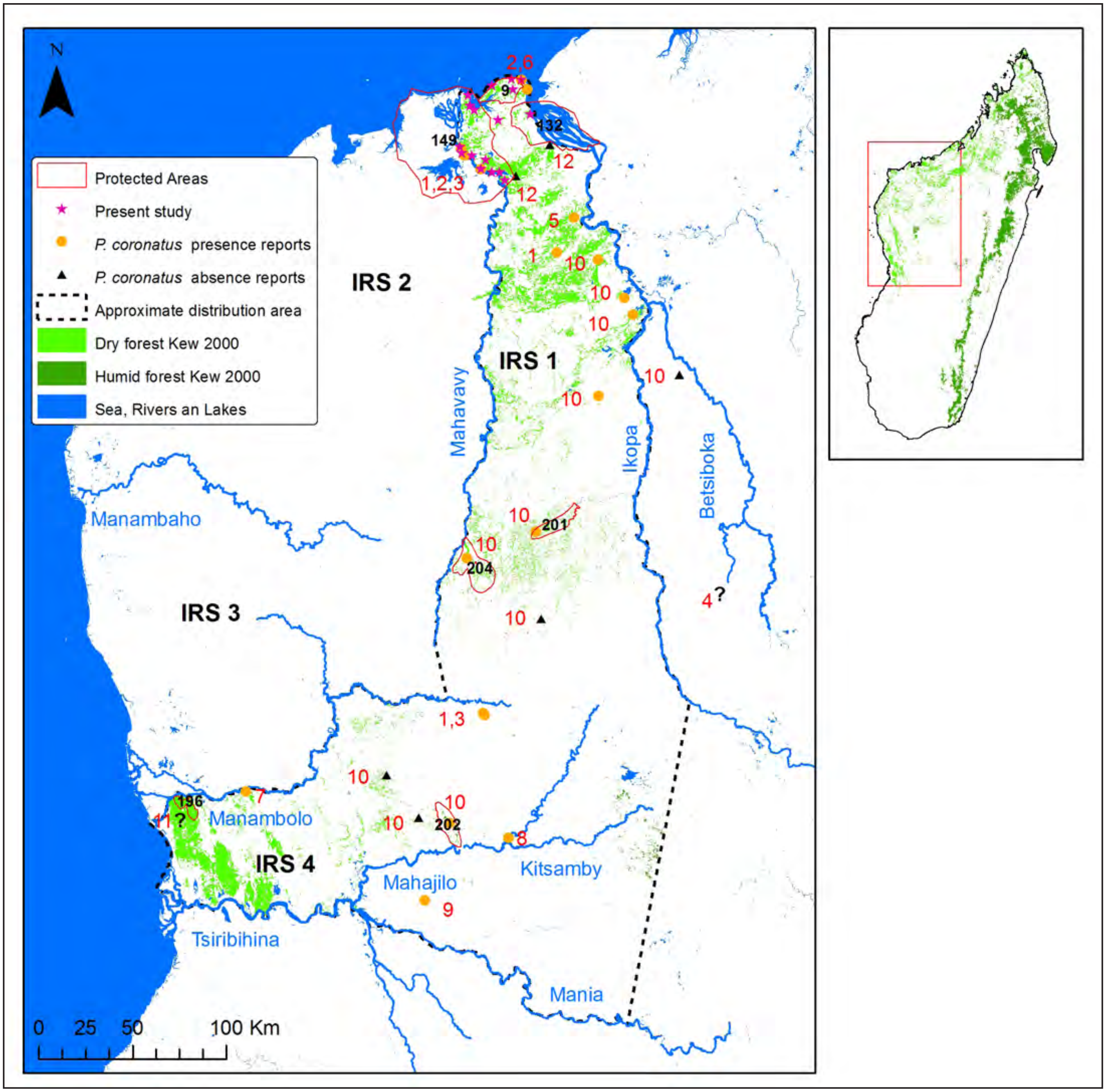

**Figure 1.** Map of the estimated area of occupancy of *P. coronatus*. This map shows the localities for *P. coronatus* in the literature and the probable distribution of the species. The references used to build this map are indicated by the red numbers whereas the corresponding orange dots identify 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'Andasilaitsaka SP; **204**: Fôret de Mahajeby 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 |
| Tsiandrarafa | 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

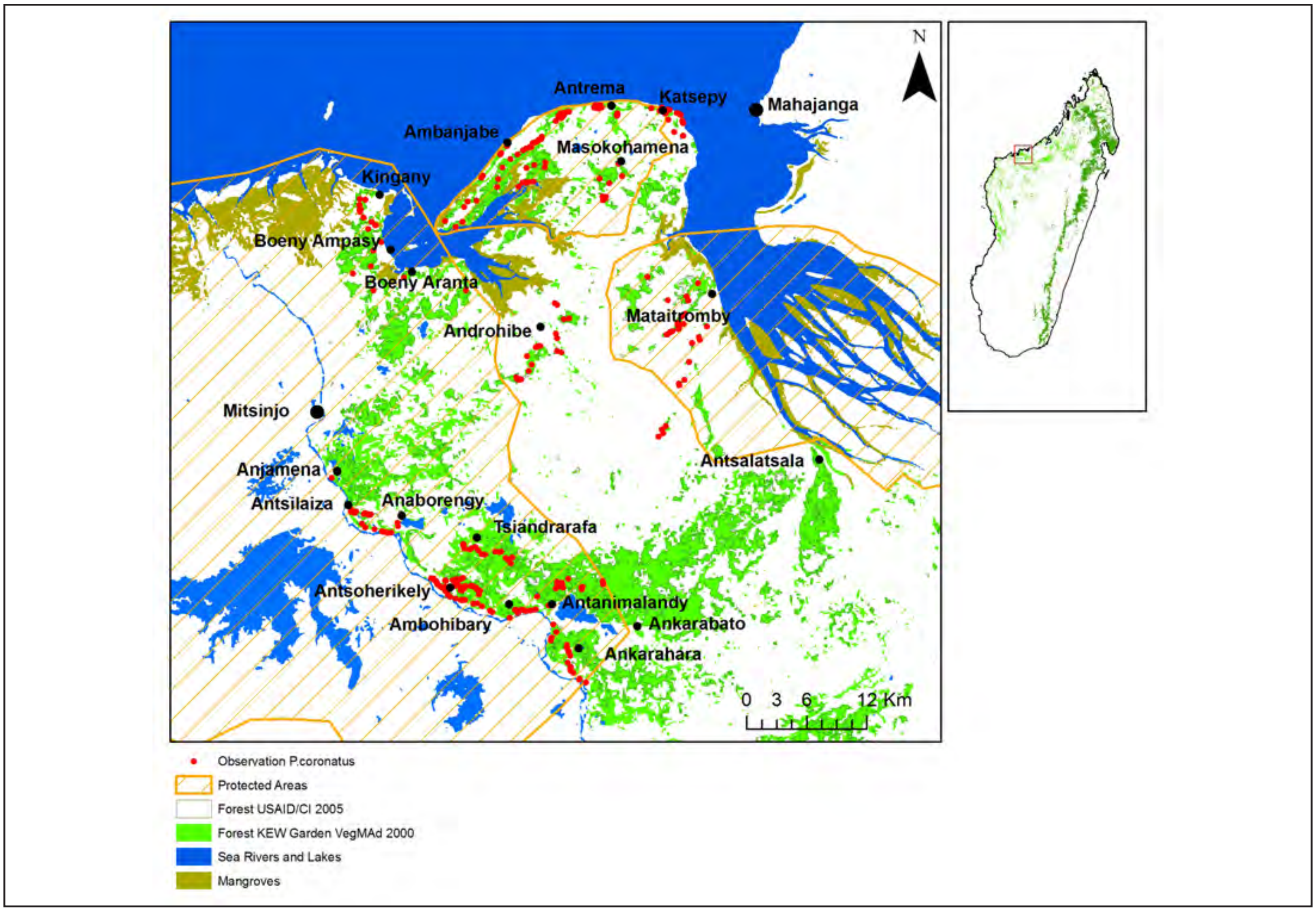

**Figure 2.** Map of the survey sites. The locations visited during our surveys with details regarding the presence of crowned sifakas. Forests outside of the range of *P. coronatus* are not shown.

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 delimitated 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 Antanimalandy 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 Antanimalandy 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 |
| Tsiandrarafa | 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 /km²) | 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 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 (km²) | b: Min. density (ind/km²) | c: Average density (ind/km²) | Minimum population size estimate (ind.) (a × b) | Maximum population 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 Badrala 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 Badrala 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-Badrala) 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 Betsiboka-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 /km²) | Estimated population size | Analysis method | Field method | Reference |
|---|---|---|---|---|---|---|
| *P. coronatus* | Anjamena | 543 | | Home range size | | Müller (1997) |
| *P. coronatus* | Antrema | >300 | | Complete census | | Pichon *et al.* (2010) |
| *P. coronatus* | Anjamena | 172.6 | | LT-DS | Müller | Müller *et al.* (2000) |
| *P. coronatus* | Katsepy | 5 | | Walk and count | Ind./estimated area | Curtis *et al.* (1998) |
| *P. coronatus* | Anjamena | 32 | | Walk and count | Ind./estimated area | Curtis *et al.* (1998) |
| *P. coronatus* | North-west | 49 to 309 | 131,852 to 220,165 | LT-DS | CDS | This study |
| *P. deckenii* | North-west | 3 to 23 | | Walk and count | Ind./estimated area | Curtis *et al.* (1998) |
| *P. verreauxi* | Kirindy | 41 to 1036 | | Complete census | | Norscia and Palagi (2008) |
| *P. coquereli* | Ampijoroa | 60 | | Home range size | | Richard (1978) in Ganzhorn (1988) |
| *P. tattersalli* | Daraina region | 34 to 90 | 11,185 to 26,011 | LT-DS | CDS | Quéméré *et al.* (2010) |
| *P. tattersalli* | Daraina region | 17 to 28 | 6,100 to 10,000 | LT-DS and Fixed Observation Point | | Vargas *et al.* (2002) |
| *P. edwardsii* | Antserananoby | 49 | | LT-DS | CDS | Kelley *et al.* (2007) |
| *P. edwardsii* | Vohibola | 2 to 73 | | LT-DS | Whitesides | Lehmann *et al.* (2006) |
| *P. edwardsii* | South-east | 7.65 | | LT-DS | Whitesides | Irwin *et al.* (2005) |
| *P. diadema* | Tsinjoarivo | 7.61 to 20.4 | | Home range size | | Irwin *et al.* (2008) |
| *P. candidus* | Makira | 1.5 to 23.1 | | LT-DS | MPD | Rasolofoson *et al.* (2007) |
| *P. candidus* | Marojejy | 40 to 90 | | LT-DS and random walking | Minimum convex polygon | Sterling *et al.* (2000) |
| *P. perrieri* | Analamenara | 3.11 | 915 | LT-DS | Whitesides | Banks *et al.* (2007) |
| *P. perrieri* | 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 | *P. coronatus* |
|---|---|
| Category: Critically Endangered: | |
| Criterion A – "Reduction in population size" >80% | ? |
| Criterion B – "Geographic range" Area of occurrence <100 km² | 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 km² | 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 overoptimistic 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 Antanimalandy, 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".

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# Acoustic Differences in Loud Calls of Decken's and Crowned Sifakas (*Propithecus deckenii* and *P. coronatus*) at Two Sites in Madagascar

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**Abstract:** Signals are important for species recognition. In this study, I examined the acoustic structure of loud calls ("Tchi-faks") in two populations of closely related lemur species in Madagascar, the Decken's and crowned sifakas (*Propithecus deckenii* and *P. coronatus*). Both populations exhibited a strong individual signature in the acoustic structure of Tchi-faks. Furthermore, Tchi-faks clearly differed in the acoustic structure between the two populations. Tchi-faks of Decken's sifakas at Bemahara were, on average, longer and have more energy in lower frequency ranges than Tchi-faks of crowned sifakas at Antrema. This variation is most likely due to anatomical differences of the vocal tract between the two species. However, loud calls of further populations need to be studied in order to understand whether the documented variation in loud calls represents species-specific signatures. In addition, to understanding whether these loud calls are important for species recognition, playback experiments are required to examine if sifakas themselves discriminate between calls of different species.

**Key Words**: vocalizations, acoustic structure, species recognition, *Propithecus coronatus*, *Propithecus deckenii*

## Introduction

Signals are essential in species recognition (Bradbury and Vehrencamp 1998). The importance of signals for the evolution and diversification of taxa has been suggested in many species (Mayr 1963; Ryan and Rand 1999; Grant and Grant 2006; Robillard *et al.* 2006). On the one hand, species-specific signals can be considered a result of sexual selection in which they function as a premating isolation mechanism (Mayr 1963; Nevo *et al.* 1987). On the other hand, species-specific vocalizations can be a result of natural selection through adaptations of the acoustic structure of calls according to habitat properties in order to optimize their transmission (Morton 1975; Ryan *et al.* 1990; Brown *et al.* 1995). In particular, acoustic signals are considered to be important parameters in species-level taxonomic analysis, ranging from crickets, anurans and birds to mammals, including primates (Macedonia and Stanger 1994; Ryan and Rand 1999; Gray and Cade 2000; Grant and Grant 2006; Cap *et al.* 2008).

Loud or long distance calls of non-human primates are the most distinctive calls in the vocal repertoire and are common in most primates (Wich and Nunn 2002). They travel over long distances and have been suggested to transmit information pertaining to inter-group spacing and territorial behavior (Marler 1967; Waser 1982; Mitani 1985; Brown *et al.* 1995). They typically have a species-specific acoustic structure and have therefore been used to infer phylogenetic relationships (Oates and Trocco 1983; Macedonia and Stanger 1994; Nietsch and Kopp 1998; Zimmermann *et al.* 2000; Konrad and Geissmann 2006; Mendez-Cardenas *et al.* 2008; Merker *et al.* 2009; Thin *et al.* 2010).

In this study, I examined acoustic variation in loud calls, the Tchi-faks, of two populations of closely related lemurs, Decken's sifaka (*Propithecus deckenii*) at Bemahara and crowned sifaka (*P. coronatus*) at Antrema in Madagascar. Tchi-faks belong to the group of loud calls and are given by sifakas during inter-group encounters, for group coordination, and sometimes in response to terrestrial predators (Fichtel and Kappeler 2002, 2011). The Verreaux's sifaka group, inhabiting the west of Madagascar, has traditionally been considered as a single species comprising four subspecies (*P. verreauxi coquereli, P. v. coronatus, P. v. deckenii*, and *P. v. verreauxi*). Recently these taxa have been elevated to species level (Pastorini *et al.* 2001, 2003; Mayor *et al.* 2004; Groves and Helgen 2007; Mittermeier *et al.* 2008, 2010), though neither chromosomal nor molecular data support a separation of *P. verreauxi*, *P. coronatus*, and *P. deckenii* (Pastorini *et al.* 2001, 2003; Rumpler *et al.* 2011).

Geographically, the *P. verreauxi*-complex occurs through much of western Madagascar with Coquerel's sifaka (*P. coquereli*) occurring north of the Betsiboka River and Verreaux's sifaka (*P. verreauxi*) occurring south of the Tsiribihina River (Tattersall 1986; Wilmé and Callmander 2006; Wilmé *et al.* 2006). The two other species, crowned sifaka and Decken's sifaka, occur in the region between these two rivers, mostly in allopatric or parapatric populations, but with several populations showing melanistic or possibly hybrid forms (Tattersall 1986; Curtis *et al.* 1998; Pastorini *et al.* 2001; Thalmann *et al.* 2002; King *et al.* 2012, 2014; Rakotonirina *et al.* 2014), and some isolated reports of possible co-occurrence of the two species (Tattersall 1982, 1988; Thalmann and Rakotoarison 1994; but see Rakotonirina *et al.* 2014 and King *et al.* 2014). It is, therefore, of particular interest to study whether these two species differ in the acoustic structure of their loud call to understand if these calls are used for species recognition, and whether they may function as a premating isolation mechanism preventing hybridization (Ryan and Rand 1999; Höbel and Gerhardt 2003; Grant and Grant 2006).

## Methods

### *Study sites and acoustic analysis*

Vocalizations (Fig. 1) were recorded of 12 adult crowned sifakas at Antrema, Katsepy, northwest Madagascar, and of nine adult Decken's sifakas at Tsingy Bemahara, western central Madagascar. The two sites are 370 km apart, and each currently supports only one of the sifaka species. Vocalizations were recorded using a Marantz PMD 670 CF-Recorder and a Sennheiser ME 80 directional microphone. Tchi-faks were elicited by presenting species-specific Tchi-faks given during group encounters via a loudspeaker (Davidactve, Visonik) hidden in the vegetation.

In order to obtain a balanced sample size, I selected 10–12 calls from each of nine Decken's sifakas and 12 crowned sifakas, resulting in 246 calls in total. Vocalizations were digitized using AVISOFT-SASLab pro 5.0.07 (R. Specht, Berlin, Germany). I visually inspected and sampled only calls of good quality and low background noise at a sampling frequency of 44.1 kHz. Next, I conducted a fast Fourier transformation (1024-pt FFT; time step: 5 ms; frequency range: 22.05 kHz; frequency resolution: 21 Hz) with AVISOFT-SASLab pro. Frequency-time spectra were analyzed with LMA 9.2, a custom software tool to extract different sets of variables from acoustic signals (Schrader and Hammerschmidt 1997). I focused on acoustic variables that characterize the general call structure and are comparable with acoustic variables that were measured in other studies characterizing the structure of mammalian vocalizations (Manser *et al.* 2001; Fichtel and Hammerschmidt 2002; Fichtel *et al.* 2005; Gros-Louis *et al.* 2008). Also, I briefly describe the acoustic variables that were used for the analysis (Fig. 1). I measured the mean duration, the mean frequency range, the mean peak frequency, and several variables of the central frequency (DFA2). The frequency range is the difference between the maximum and minimum frequency of a call. The peak frequency is the frequency with the highest amplitude. In order to characterize the frequency distribution of the call, I measured the statistical distribution of the frequency amplitudes across the spectrum. The frequency at which the cumulative sum of the frequency amplitudes (starting with the lowest frequency in the spectrum) reaches the median of the total distribution is the central frequency. Here, I measured the maximum, minimum and median of the central frequency. Acoustic variables entered in the analysis were revealed by Pearson's correlation analysis. I excluded variables exhibiting a correlation coefficient higher than 0.8; the remainder were kept and entered into the analysis.

### *Statistical analysis*

I used a permuted discriminant function analysis (pDFA, Mundry and Sommer 2007) to identify acoustic differences of Tchi-faks. The discriminant function analysis provides a classification procedure that, based on the discriminant function, assigns each call to its appropriate group (correct assignment) or the other group (incorrect assignment). In order to cross-validate the discriminant functions that were generated for contexts, I used up to eight calls of each individual to create the discriminant function and up to four calls of each individual for the cross-validation of the original discriminant function. Since the discriminant function analysis is sensitive to number of variables entered in the analysis and to unbalanced sample sizes, I used a permuted discriminant function analysis to statistically evaluate the classification result. The permuted discriminant function analysis first creates 100 random selections of calls of the original data set to control for any possible random effects of call selection. In the next step 1000 randomized data sets are created. The

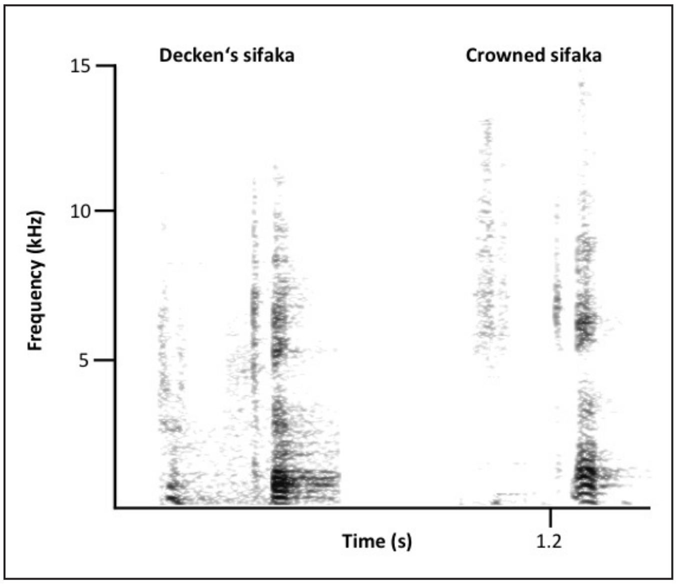

**Figure 1.** Spectrograms of Tchi-faks of Decken's and crowned sifakas.

permutation algorithm randomizes subjects between contexts, by this means controlling for the factorial (nested) structure of the data with subjects being nested within contexts. In the last step the permuted discriminant function analysis compares the mean correct assignment of the 100 original data sets with the correct assignment of the 1000 randomly created data sets (Mundry and Sommer 2007).

In total, I conducted three different permuted discriminant function analyses. Two permuted discriminant function analyses were conducted to characterize individual differences in the acoustic structure of the Tchi-faks of crowned and Decken's sifakas. The third discriminant function analysis was conducted to characterize differences in the acoustic structure of Tchi-faks between the two sifaka populations. For subsequent analysis of single acoustic variables such as duration and frequency range, I fitted a LMM with species as a fixed factor and ID as a random factor using the R software (R Development Core Team, Vienna, Austria, 2010) with the lme-package (Zuur *et al.* 2009).

## Results

### *Decken's sifaka Tchi-faks: acoustic structure and individuality*

Tchi-faks of Decken's sifakas at Bemahara were characterized by a mean duration of 267 ± 52 ms (Fig. 1; Table 1). They had a frequency range of, on average, 3552 ± 1014 Hz, and a central frequency of, on average, 2347 ± 576 Hz. The discriminant function analysis revealed a correct assignment of calls to each of the nine individuals of 85% and a correct assignment of the cross-validation of 78%. The correct assignment of the original data sets differed significantly from the correct assignment of the random data sets (P = 0.001). The correct classification of the remaining calls for the cross-validation of the original data set did not differ from the random data sets (P = 1).

**Table 1.** Mean (± SD) of the analyzed acoustic variables of the Tchi-faks of Decken's sifakas at Bemahara and crowned sifakas at Antrema, Madagascar.

| Acoustic variables | Decken's sifakas | Crowned sifakas |
|---|---|---|
| Duration | 267 ± 52 ms | 218 ± 63 ms |
| Maximum central frequency | 5614 ± 1051 Hz | 7051 ± 875 Hz |
| Minimum central frequency | 1055 ± 131 Hz | 1154 ± 214 Hz |
| Median central frequency | 2347 ± 576 Hz | 4322 ± 1237 Hz |
| Mean frequency range | 3552 ± 1014 Hz | 4698 ± 2131 Hz |
| Mean peak frequency | 1097 ± 422 Hz | 1672 ± 704 Hz |

### *Crowned sifaka Tchi-faks: acoustic structure and individuality*

Tchi-faks of crowned sifakas at Antrema were characterized by a mean duration of 219 ± 63 ms (Fig. 1; Table 1). They had a frequency range of, on average, 4698 ± 2131 Hz, and a central frequency of, on average, 4322 ± 1237 Hz. The discriminant function analysis revealed a correct assignment of calls to each of the 12 individuals of 69% and a correct assignment of the cross-validation of 61%. The correct assignment of the original data sets differed significantly from the correct assignment of the random data sets (P = 0.001). The correct classification of the remaining calls for the cross-validation of the original data sets did not differ from the random data sets (P = 1).

### *Comparison of the acoustic structure of Tchi-faks between the two populations*

The discriminant function analysis revealed a correct assignment of calls to the two populations of 96% and a correct assignment of the cross-validation of 99%. The correct assignment of the original data sets differed significantly from the correct assignment of the random data sets (P = 0.001). In addition, the remaining calls withheld for the cross-validation of the original data sets were also better correctly classified than the random data sets (P = 0.001). A subsequent LMM revealed that Tchi-faks between the two populations differed significantly in all acoustic variables, except the mean frequency range (Fig. 2a, 2b; Table 2). Thus, calls clearly differed in their acoustic structure between the species at the two locations sampled. Calls of Decken's sifakas at Bemahara were, on average, longer and had more energy in lower frequency ranges than calls of crowned sifakas at Antrema.

**Table 2.** Estimate, Standard errors and p-value for each Linear Mixed Effects Model.

| Acoustic variables | | Estimate | Std. Error | p-value |
|---|---|---|---|---|
| Duration | Intercept | 216.85 | 15.41 | <0.001 |
| | Species | 49.61 | 23.53 | 0.048 |
| Maximum central frequency | Intercept | 7039.67 | 211.84 | <0.001 |
| | Species | -1423.35 | 323.41 | <0.001 |
| Minimum central frequency | Intercept | 216.85 | 15.41 | <0.001 |
| | Species | 49.61 | 23.53 | 0.048 |
| Median central frequency | Intercept | 4297.03 | 270.61 | <0.001 |
| | Species | -1956.18 | 413.28 | <0.001 |
| Mean frequency range | Intercept | 4644.17 | 466.06 | <0.001 |
| | Species | -1092.82 | 711.77 | 0.14 |
| Mean peak frequency | Intercept | 1671.34 | 124.47 | <0.001 |
| | Species | -572.18 | 189.98 | 0.007 |

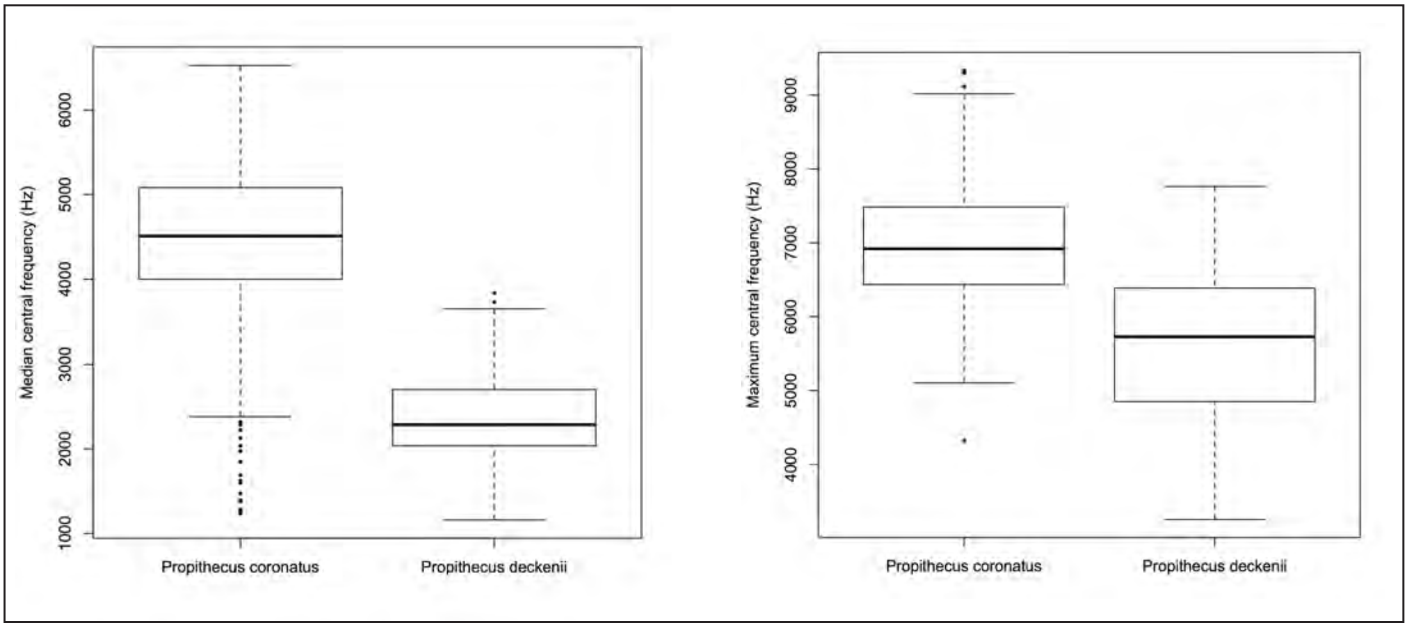

**Figure 2.** Boxplot of (a) the median central frequency and (b) the maximum frequency of Tchi-faks of crowned sifakas (*Propithecus coronatus*) at Antrema and Decken's sifakas (*Propithecus deckenii*) at Bemahara. Represented are median (black bars), interquartile range (boxes), upper and lower hinge (whiskers) and outliers (circles).

## Discussion

This study shows that the Tchi-faks of both Decken's and crowned sifakas are highly individually distinctive. Individual distinctiveness in vocalizations has also been shown in other lemur species (Macedonia 1986; Oda 2002; Gamba *et al.* 2012). In addition, the acoustic structure of the Tchi-faks clearly differs between the two locations sampled. They differed in duration but also in four of the five measured frequency-related variables—Tchi-faks of Decken's sifakas at Bemahara are, on average, longer and have a lower pitch as measured by lower frequency values of the maximum, minimum and the median of central frequency and peak frequency than those of crowned sifakas at Antrema. This variation might be the result of ecological factors, genetic differences and/or anatomical differences.

As habitat type affects sound transmission (e.g., Wiley and Richards 1978), animals are expected to adapt their vocal behavior to the structural and acoustic properties of the environment they inhabit ("The habitat adaption hypothesis," Morton 1975). Some studies have found support for this hypothesis (Ryan and Brennowitz 1985; Ey *et al.* 2009), whereas others have not (Brown *et al.* 1995; Daniel and Blumstein 1998). Since the habitat at both sample locations for this study is characterized by dry deciduous forest, it is unlikely that ecological factors will explain diversification of the Tchi-fak calls between the two sifaka populations.

In some primates, acoustic differences in vocalizations have been shown to be in concordance with genetic differences (Merker *et al.* 2009; Thin *et al.* 2010; Markolf *et al.* 2013). Since Decken's and crowned sifakas do not exhibit large differences in mitochondrial DNA (Pastorini *et al.* 2001, 2003; Rumpler *et al.* 2011), a genetic basis underlying structural differences in Tchi-faks is rather unlikely. However, more research combining analyses of molecular and acoustic data are required to understand whether the described acoustic differences may have a genetic base.

The anatomy of the vocal tract influences the acoustic structure of vocalizations in a variety of species (Fitch 1997; Reby *et al.* 2005; Gamba and Giacoma 2006; Charlton *et al.* 2009). For example, in rhesus macaques (*Macaca mulatta*) formant frequency dispersion is correlated with vocal tract length and body size (Fitch 1997). Analysis of sifaka museum specimens show that crowned and Decken's sifakas differ in several cranio-dental measurements as for example bicanine and biorbital breadth or skull length measured as the condylobasal length: crowned sifakas have a more deepened and much broader snout than Decken's sifakas (Groves and Helgen 2007). Thus, acoustic differences in call structure might be due to different shapes of the vocal tract.

However, to understand if these calls are important for species recognition, further populations need to be studied to analyze potential geographical variation within species. For example, in Verreaux's sifakas the acoustic structure of Tchi-faks clearly differed in three geographically separated populations, suggesting that there is strong geographical variation in this closely related species (Fichtel, unpubl. data). Divergence in acoustic signals between populations can lead to species recognition failure, reproductive isolation, and speciation. In some species individuals diverge more in call structure in sympatry than in allopatry (Höbel and Gerhardt 2003; Kirschel *et al.* 2009). Such character displacement occurs where the ranges of two closely related species overlap, and morphological, ecological, or behavioral traits diverge in sympatry, facilitating coexistence of species in natural communities (Brown and Wilson 1956; Grant and Grant 2006).

Finally, to understand whether sifaka calls may function as a premating isolation mechanism, playback experiments are required to demonstrate whether sifakas discriminate between calls of different species, and use these calls for species recognition to avoid hybridization. These results would have important implications for future conservation management plans.

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# Social Behavior and Dominance of the Crowned Sifaka (*Propithecus coronatus*) in Northwestern Madagascar

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**Abstract:** We carried out a study of the social behavior and dominance hierarchy in three groups of crowned sifaka (*Propithecus coronatus*) in the Antrema Forest Station in north-west Madagascar. Data were collected from April to June 2009 and October to November 2009 using all-occurrence sampling. During 273 hours of observation, the majority of social behaviors observed were grooming interactions (39%), followed by agonistic behavior (25%), play (19%), scent-marking (9%), call-localization (5%) and approach (3%). A social hierarchy was maintained in the groups of *P. coronatus*, with females dominating the males. Although different groups of *P. coronatus* defended their territories against other neighboring groups of the same species, the most frequently observed outcome of intergroup encounters was tolerance. In addition, we detected no significant change of sifaka behavior during interspecific encounters with rufous brown lemur (*Eulemur rufus*) or with mongoose lemur (*Eulemur mongoz*), suggesting these two species live in total sympatry with *P. coronatus*.

**Key Words:** *Propithecus coronatus*, social behaviors, female dominance, intergroup encounter, interspecific relationships, Antrema

## Introduction

The social behavior of primates has been the subject of many studies published across several decades (Crook and Gartlan 1966; Clutton-Brock and Harvey 1977; Dunbar 1988). Hierarchical interactions can be observed in gregarious and territorial primates (Cords 1987; Stanford 1991; Yeager 1992). In this case, different relationships between individuals of a group or between different groups can be affected by the dominance hierarchy. In most non-human primates social dominance is usually male-biased, e.g., *Cebus capucinus*, *Alouatta* spp. *Presbytis* spp., *Colobus* spp., *Cercopithecus* spp., *Nasalis larvatus*, *Erythrocebus patas* and *Gorilla gorilla* (Cords 1987; Crockett and Eisenberg 1987; Robinson and Hanson 1987; Struhsaker and Leland 1987; Stanford 1991; Yeager 1992). However, in some gregarious lemur species, the females dominate males (Richard and Nicoll 1987; Sauther *et al.* 1999) and group size is relatively small (Kappeler 1997). Although several behavioral studies have shown that social activities represent only a small part of the daily activity budget of lemurs (Hemingway 1999; Charrier *et al.* 2007; Pichon *et al.* 2010), these activities could be important if they are beneficial to individuals and/or help maintain social structure.

There are no published accounts of the social relationships of crowned sifaka (*Propithecus coronatus*) in the wild. The crowned sifaka is classified as Endangered by the IUCN (2012; Salmona *et al.* in press). It is a diurnal, folivorous, medium-sized lemur, which lives in groups of up to eight individuals in the dry forests of north-western and central-western Madagascar (Mittermeier *et al.* 2010; Rakotonirina *et al.* in press; Salmona *et al.* in press). Here, we present the results of observations conducted on three groups of crowned sifakas in the Antrema Forest Station of north-western Madagascar. The aim of the study was to improve our understanding of the social behavior of the species, including patterns of dominance hierarchy.

## Methods

### *Study site*

The Antrema Forest Station is included in the network of protected areas in Madagascar. Four lemur species are present at the site in addition to *P. coronatus*: two diurnal (rufous brown lemur *Eulemur rufus* and mongoose lemur *Eulemur mongoz*) and two nocturnal (Antafia sportive lemur *Lepilemur aeeclis* and a mouse lemur *Microcebus* sp.) (nomenclature following Mittermeier *et al.* 2010). Located in the north-west of Madagascar, on the Katsepy Peninsula, the station covers 12,270 ha; mostly of dry forest on sandy soil but including a 1,000-ha marine park. Ecologically, it belongs to the Western area (Humbert 1955), the vegetation of which is characterized by species particularly adapted to drought, including *Dalbergia, Commiphora* and *Hildegardia.* Our study was conducted in the 24-ha Badrala forest fragment (15°45.665'S, 46°12.300'E), located 3 km from the Antrema village. Fifteen groups of sifaka have been identified living in this fragment.

### *Observation protocol*

Data were collected from April to June and from October to November 2009 on three groups of regularly monitored sifakas: G1 (two males and two females), G2 (three males and two females) and G3 (three males and three females). Each sifaka was identifiable through their unique facial markings.

Social behavior was studied using all-occurrence sampling (Altmann 1974) and was conducted in parallel with an investigation into diet and behavior (Pichon *et al.* 2010). Observations were made between 06:30 h and 18:00 h (or 18:30 h according to visibility). The three main types of social behaviors we recorded were affiliative (grooming interactions, approach, play and call-localization), agonistic and scent-marking (Table 1). To assess social dominance, the frequency of threats and/or avoidance between individuals was noted. Once an aggression was observed, the identity and sex of the individual *director* (i.e., who initiated the attack) and *receiver* (i.e., who suffered the attack) were noted, together with the context in which the aggression occurred. The individual with the highest rate of aggression toward other group members was considered dominant. During intergroup encounters, the behaviors (for example, alarm, affiliative, aggression, or other) of all individuals of the group were recorded. The behaviors of the entire group were also noted during interspecific encounters.

### *Hierarchical dominance*

Dominance was estimated by the number of aggressions recorded among agonistic behaviors (slapping, biting, stealing food) in which actors were identified. The dominant sex was estimated by comparing numbers of aggressions initiated against others of the opposite sex using a chi-square test ($\chi^2$).

**Table 1.** Social behaviors recorded during the study of three groups of *Propithecus coronatus*.

| | |
|---|---|
| Agonistic* | Slapping, biting, stealing food, avoidance, escape, recoil against another individual |
| Grooming interactions** (allogrooming and mutual grooming) | Affiliative interactions to groom another individual to remove dirt and ectoparasites in the body (hygienic function), to reduce stress, and to reinforce the social structure (social function) |
| Approach* (searching for proximity) | Individual going to, moving toward, getting close to, sitting or lying close to a congener |
| Call-localization | Search for other members of the group while making some vocalizations |
| Play* | Provocation action, pursuit, fight or other |
| Scent-marking* | Action to smell or make a scent mark with the anogenital gland (female and male) or chest gland (male) |

*Definition modified from Moral (2009).
**Definition modified from Morelli (2008).

## Results

### *Social behavior*

During 273 hours of continuous sampling we observed 173 social interactions. Grooming was most frequently observed (39% of cases), followed by agonistic behaviors (25%) and play (19%). Scent-marking, call-localization and approach were rarely observed (9%, 5% and 3%, respectively) (Fig. 1).

### *Hierarchical dominance*

Using the number of aggressive events recorded during agonistic behaviors in which all actors were identified, the direction of aggressive acts clearly showed a dominant female in each of the three groups. Half of the aggressions (51%; n = 39) were initiated by females and were directed toward males. However, tests on the overall data showed that females attacked males more than the reverse. These results suggest a female dominance over males for all groups ($\chi^2 = 6.593$, $p < 0.0103$). For group G1, the dominant individual was the female F2, and she initiated 65% (n = 20) of attacks in the group (Table 2). The dominant individual of group G2 was the female F1 (63% of attacks, n = 8; Table 3), and in group G3 female F1 was dominant (73% of attacks, n = 11; Table 4).

More aggressive interactions were observed in the smallest group, G1 (n = 20), compared to the two other groups (n = 8 for G2 and n = 11 for G3). Also the number of intersex aggressions (female-male and male-female) was higher in G1 (n = 11) than in G2 (n = 5) or G3 (n = 9). Twenty-one percent of all aggressive acts (intra- and intergroup) were food-related, that is to say,

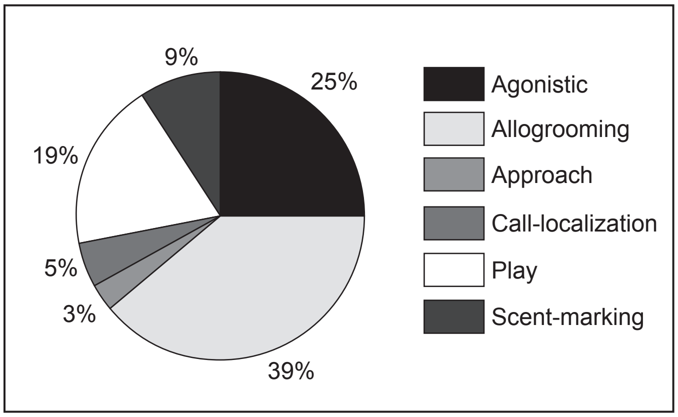

**Figure 1.** Proportions of social behaviors of crowned sifakas recorded during our study (n = 173).

**Table 2.** Dominance matrix for group G1 (♀: female; ♂: male). Dominant individual: female F2 with 63% (n = 20) of aggression within the group.

| **Director**<br>**Reciever** | **F1♀** | **F2 ♀** | **M1♂** | **M2♂** |
|---|---|---|---|---|
| F1♀ | ■ | 5 | 2 | |
| F2♀ | | ■ | | |
| M1♂ | | 6 | ■ | 1 |
| M2♂ | 1 | 2 | 3 | ■ |

**Table 3.** Dominance matrix for group G2 (♀: female; ♂: male). Dominant individual: female F1 with 63% (n = 8) of aggression within the group.

| **Director**<br>**Receiver** | **F1♀** | **F2♀** | **M1♂** | **M2♂** | **M3♂** |
|---|---|---|---|---|---|
| F1♀ | ■ | | | 1 | |
| F2♀ | 1 | ■ | | | |
| M1♂ | 1 | | ■ | | |
| M2♂ | 2 | | | ■ | |
| M3♂ | 1 | | 1 | 1 | ■ |

**Table 4.** Dominance matrix for group G3 (♀: female; ♂: male). Dominant individual: female F1 with 73% (n = 11) of aggression within the group.

| **Director**<br>**Receiver** | **F1♀** | **F2♀** | **F3♀** | **M1♂** | **M2♂** | **M3♂** |
|---|---|---|---|---|---|---|
| F1♀ | ■ | | | | | |
| F2♀ | | ■ | | | | |
| F3♀ | 1 | | ■ | 1 | | 1 |
| M1♂ | 2 | | | ■ | | |
| M2♂ | 3 | | | | ■ | |
| M3♂ | 2 | | | 1 | | ■ |

the director or the receiver of the attack was either feeding or approaching food. Otherwise, the contexts were variable.

### *Intergroup relationships*

Only 19 intergroup encounters were recorded, giving a rate of 0.07 encounters per hour. Meeting areas were often limited to up to 10 m. In most cases (63%), meetings with other groups did not affect the activity of the observed group. Sometimes an intergroup encounter was followed by a temporary interruption of the activities of group members to observe the neighboring group without direct contact between individuals. In the remaining cases (37%), reactions included aggressive pursuit of individuals of the other group, scent-marking, flight of the focal group or jumping from tree to tree, all of which may be attributed to the defense of territory.

### *Interspecific relationships*

Interspecific encounters were very rare, with two recorded cases each with *Eulemur rufus* and *Eulemur mongoz*. In all cases, the presence of these two species did not seem to affect the behavior of the crowned sifakas. An encounter with a dog, however caused flight and temporary splitting of the focal sifaka group.

## Discussion

This study describes social behaviors observed in three crowned sifaka groups in the Antrema Forest Station over a five-month period. As our study was conducted in parallel with other studies, we probably overlooked some interactions, and some behaviors were not observed due to the timing of our study. Lactation, for example, was not observed because no young were present during our field observations, and no reproductive behavior was observed as the study did not take place during the mating period (the mating period of the closely-related Verreaux's sifaka *P. verreauxi* in Kirindy, an environment similar to Antrema, is between late January and March; Kraus *et al.* 1999).

Social organization and behavior of primates are influenced in part by the distribution of resources (van Schaik and van Hooff 1983; van Schaik 1989; Barton *et al.* 1996). The highly seasonal environment at Antrema would, therefore, be expected to result in different social behaviors of *P. coronatus* between the dry and wet seasons, and we recommend future studies of social behavior in Antrema to investigate this.

The dominance of female crowned sifaka observed in the present study suggests that the social organization of this species is similar to that reported in other sifakas such as *P. verreauxi* (see Richard and Nicoll 1987), diademed sifaka *P. diadema* (see Hemingway 1999) and Milne-Edwards' sifaka *P. edwardsi* (see Pochron *et al.* 2003). In this study, we used only aggressive behaviors to measure the dominance hierarchy. Since the rate of aggression in this species is low, however, there could be other behaviors, more complex and difficult to identify, that indicate dominance; two possibilities would be scent-marking and submission (Kraus *et al.* 1999; Lewis 2006; Pochron *et al.* 2005). Our analysis of the contexts in which aggressions were initiated by female crowned sifakas, with most observed aggressions happening outside the feeding phases, confirms that female dominance in lemurs is not related only to priority access to resources (Kappeler 1990).

Despite the limited number of observation days, the low intergroup encounter rate we report is consistent with observations in other sifaka species (Irwin 2006; Benadi *et al.* 2008). On the other hand, the reactions of all individuals of *P. coronatus* observed during intergroup encounters in Badrala differed from those reported by Irwin (2006) for *P. diadema* in Tsinjoarivo and by Benadi *et al.* (2008) for *P. verreauxi* in Kirindy. In these two studies the most frequently observed reactions were agonistic among neighboring groups. In our study of *P. coronatus,* even though territorial defense was evident in some intergroup encounters, tolerance between groups was most frequently observed. This may be due to neighboring groups being related or due to a mutual habituation of the groups in response to small forest fragments and a high population density (Pichon *et al.* 2010; Salmona *et al.* in press).

Concerning interspecific relationships, the tolerance we observed in *P. coronatus* when encountering *Eulemur rufus* and *E. mongoz* is probably associated with their different diets. While *P. coronatus* is folivorous (Pichon *et al.* 2010), *E. rufus* and *E. mongoz* are frugivorous-folivorous (Curtis and Zaramody 1998; Simmen *et al.* 2003). However, the reaction of crowned sifaka that we observed during an encounter with a dog suggests that research is needed to determine whether the presence of dogs in Badrala Forest is a threat to the sifaka population.

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# The European Captive Population of Crowned Sifaka: 25 Years of Management

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**Abstract:** A European Endangered Species Program (EEP) was set up for the crowned sifaka (*Propithecus coronatus*) in 2007, and the European captive population was identified as a conservation priority for the species during the first technical meeting on its conservation in 2011. In this article I trace the history of the European population over 25 years of management, and report on the main problems encountered during this time: the lack of females, high mortality rates of infants, and the management, of surplus males. I also present general information on the demography and genetics of the captive population, as well the principle findings of studies on the biology of the species in captivity, including, particularly, observations on reproduction: number and duration of estrus, inter-estrus interval, detection of estrus by the change in behavior of both sexes, data on fertility by age in both sexes, age at first estrus and first birth, gestation length, body weight at birth, and interbirth interval. Records of the breeding success of each female and for each pair are summarized: number of offspring, infant mortality rate, age at first birth, specific management of each female/pair, and interbirth interval. I discuss the contribution of the European holders, including the Parc Zoologique de Paris, to the conservation of the crowned sifaka through their strong involvement in *in situ* projects, among them a metapopulation project recently initiated by the EEP. In this project, the European captive population is included in a global management plan for the species, in particular to contribute to the management of the smallest wild populations living in isolated fragments of forest. The educational activities developed by the European holders and then by the EEP increase awareness and knowledge of the species and facilitate fundraising for the *in situ* projects supported.

**Key words:** Crowned sifaka, captive breeding program, captivity, research in captivity, *in situ* conservation, education

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## Introduction

The crowned sifaka, *Propithecus coronatus*, is endemic to Madagascar and classified as Endangered on the IUCN Red List of Threatened Species (IUCN 2012; Salmona *et al.* 2014). The European captive population of crowned sifaka was founded in the late 1980s by the Parc Zoologique de Paris. During the following 25 years very few zoos managed to successfully maintain and breed this species in captivity: only four European zoos achieved successful births. Outside of Europe, the species is kept in only one zoo in Madagascar, where it has never bred (single-sex group).

All crowned sifakas in Europe are part of a European Endangered Species Programme (EEP), a breeding program initiated and coordinated by the Parc Zoologique de Paris. The observations that were made over 25 years, especially at the Parc Zoologique de Paris — the institution with the most experience in the husbandry of crowned sifakas — have improved our knowledge of the species and its management in captivity. Additionally, some zoos that hold the species are involved in *in situ* conservation projects, partly through the initiative of the EEP. For example, a metapopulation conservation project was initiated by European zoos during an EEP meeting in 2007. The project was subsequently approved at the first technical meeting for the conservation of the crowned sifaka, with the captive population in Europe being identified as an important element (MEF/GERP/TAF 2011). This article presents information on 25 years of management and research of the European captive population, and on the activities of the breeding program and its participants for the conservation of the crowned sifaka.

## History of the Captive Population

The first crowned sifakas were imported to Paris from Madagascar in 1987—one male and three females. Only one female survived from this first group. A second group arrived in 1993, consisting of two females and two males. These five individuals were the founders of today's captive population, of which two were still alive in 2012. These animals and their descendants were entrusted to the Parc Zoologique de Paris by the Malagasy Government under an "accord de collaboration et d'assistance" signed in 1993 to found a captive breeding program. This agreement aimed to: a) establish a captive population for potential reinforcement projects for the wild population; and b) develop research activities in order to contribute to our knowledge of the species.

In 2007, the Parc Zoologique de Paris proposed that it would establish and coordinate a European Endangered species Program (EEP) for the crowned sifaka. EEPs were created in the mid 1980s to develop sustainable captive populations of the most endangered species (Nogge 2003). They are managed by the European Association of Zoos and Aquaria (EAZA); an association created in 1988 that currently has 322 members in 36 countries. The EEPs are managed by appointed coordinators from EAZA institutions. They are assisted by a Species Committee, usually composed of representatives of the holding institutions as well as advisors (on conservation or veterinary medicine, for example). The EEP coordinator ensures that the population fulfils the roles (for example, conservation, research, education) and reaches the targets (for example, population size and genetic diversity) identified in the Regional Collection Plan (RCP). The RCP is established by the respective EAZA Taxon Advisory Group (TAG). The objectives of the crowned sifaka EEP are established by the Prosimian TAG.

## Studbook Management and Analysis

Records of every individual sifaka currently or historically included in the EEP population are held and regularly updated using the studbook management database software SPARKS v1.6 (Single Population Analysis & Records Keeping System, developed by ISIS; Scobie 1997). Data from SPARKS are exported to the studbook analysis software PMx (Lacy *et al.* 2012) for calculation and analysis of demographic, kinship, and inbreeding measures. Results presented in this paper are based on studbook data updated to mid 2011, complemented by qualitative observations of the captive animals.

## Size and Composition of the European Captive Population

The size of the European captive population of crowned sifaka has evolved from 1987 to 2011 (Fig. 1). Of four sifakas imported in 1987, only one was still alive in 1992. In 1993 another four sifakas were imported. The population subsequently increased from 1994 to 2005, but has been decreasing overall since 2005; especially the number of females has fallen dramatically (Fig. 1). As of mid 2011, the European studbook has registered a total of 53 animals (30 males, 20 females, and three aborted fetuses) since the start of the program. Seventeen of these (13 males, 4 females) were still alive in 2011, and were held in six institutions (Roullet 2011). There are currently three mixed-sex groups, two of which are breeding groups, whilst the third is composed of two young animals that should become mature before the next breeding season.

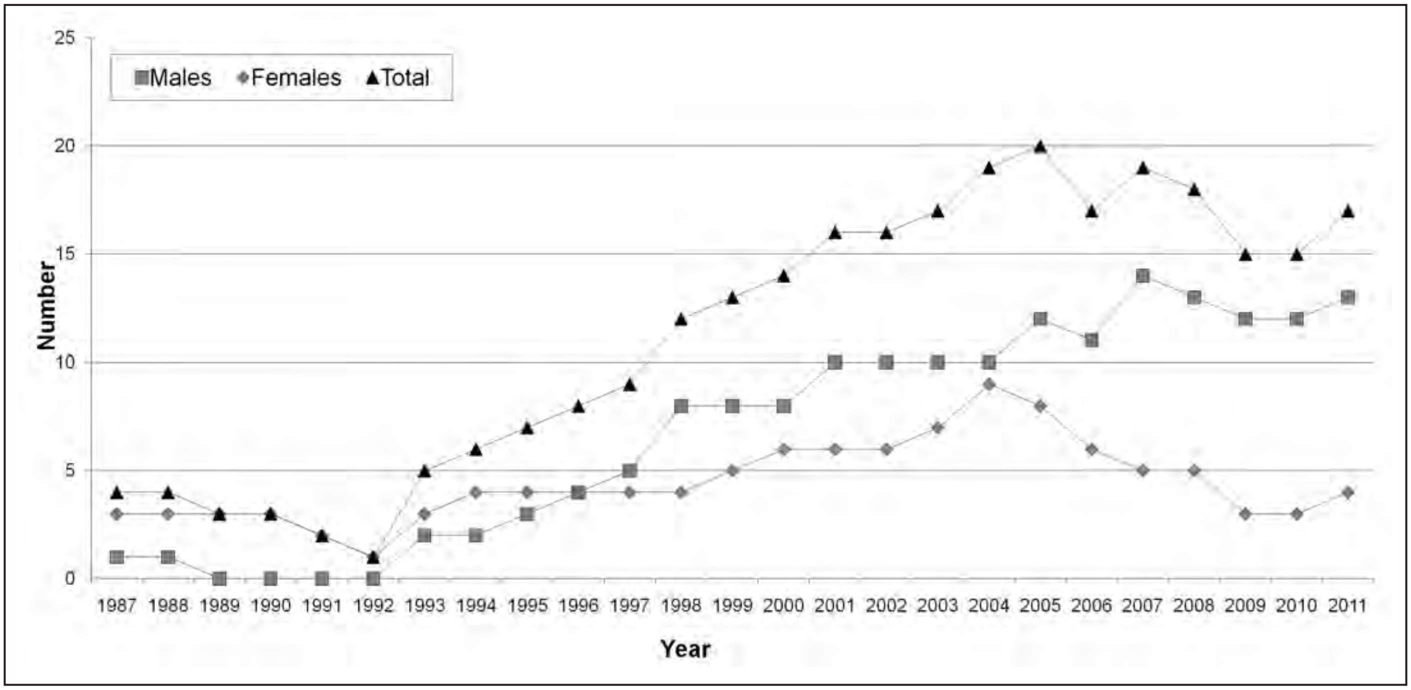

**Figure 1.** Evolution of the European captive population of crowned sifaka (*Propithecus coronatus*) from 1987 to 2011.

Current retained gene diversity (as a percentage of the genetic diversity present in the wild-caught founder population, excluding the wild-caught individuals that did not reproduce) is 84.4%, which is lower than the target of 90% but still fairly high considering the low number of founders. Inbreeding coefficients are all zero, but population mean kinship (a measure of the average degree of relatedness between individuals) is 0.145 (Table 1), a rather high value due to the low number of founders.

The founder representation (i.e., the contribution of each founder to the current living population) varies in the five founders (Fig. 2). This is due to the unequal contributions of the founders and their offspring. The situation is improving, however, with two of the three least-represented founders (founders 7 and 8) still able to breed.

**Table 1.** Inbreeding coefficients (F) and Mean kinship values (MK) of the living captive crowned sifakas (*Propithecus coronatus*). Animals with a lower mean kinship values have relatively fewer genes in common with the rest of the population, and are therefore more genetically valuable in a breeding program.

| Studbook number | Sex | Age | F (Inbreeding coefficient) | MK (Mean kinship) |
|---|---|---|---|---|
| 7 | M | 25* | 0 | 0.092 |
| 8 | F | 22* | 0 | 0.050 |
| 13 | M | 15 | 0 | 0.175 |
| 14 | M | 14 | 0 | 0.175 |
| 16 | M | 13 | 0 | 0.175 |
| 17 | M | 12 | 0 | 0.083 |
| 18 | F | 12 | 0 | 0.200 |
| 23 | M | 11 | 0 | 0.154 |
| 24 | M | 10 | 0 | 0.183 |
| 36 | M | 5 | 0 | 0.129 |
| 37 | M | 5 | 0 | 0.162 |
| 38 | M | 5 | 0 | 0.154 |
| 43 | M | 3 | 0 | 0.162 |
| 44 | F | 3 | 0 | 0.154 |
| 45 | M | 3 | 0 | 0.129 |
| 50 | M | 1 | 0 | 0.162 |
| 51 | F | 1 | 0 | 0.133 |

*Estimated age, as they are wild-born.

## Age-specific Survival and Fertility

Annual mortality rates by age-class (Table 2) show high infant mortality, no recorded male mortality from age 4 to 11 or female mortality from age 6 to 13, and increasing adult mortality thereafter. The EEP data show that females can live to at least 20 years, and males to at least 25 years. However, the deaths of several adults have been related to transfers. Captive male Coquerel's sifakas (*Propithecus coquereli*) can live to thirty years, but females die younger (Weigl 2005; Duke Lemur Center, pers. comm.).

Age-specific fertility rates show an onset of fertility at age 3 (Table 2), although high mortality rates mean that only 54% of males and 36.4% of females survive to the age of first reproduction (Table 2). Fertility increases at age 4 for the males and 6 for the females (Table 2).

## Reproduction

The first birth in the crowned sifaka EEP population took place in 1994. There have now been 27 males and 15 females born, plus three aborted pregnancies, a ratio of 1.8 males for each female newborn. Of the 42 infants born alive, seventeen (40.5%) died a few days after birth, illustrating that the first three days following birth are critical to infant survival prospects. Offspring survival rate to three days after birth is variable between females, with one of the population founders ("Daya") being the most successful at 80%, whilst others have only 50% success (Table 3).

As in the wild (Richard 1974, for *P. verreauxi*), there is a pronounced breeding season in captivity. Births occurred from November to April, most (68%) of them in December

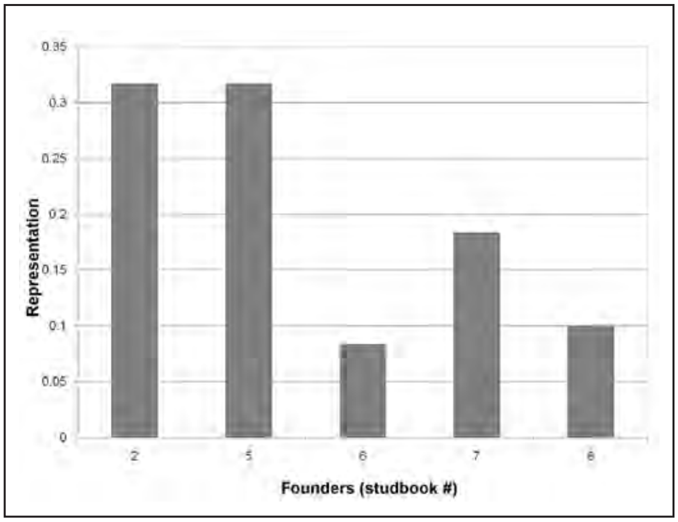

**Figure 2.** Founder representation in the European captive population of crowned sifaka (*Propithecus coronatus*) 2011.

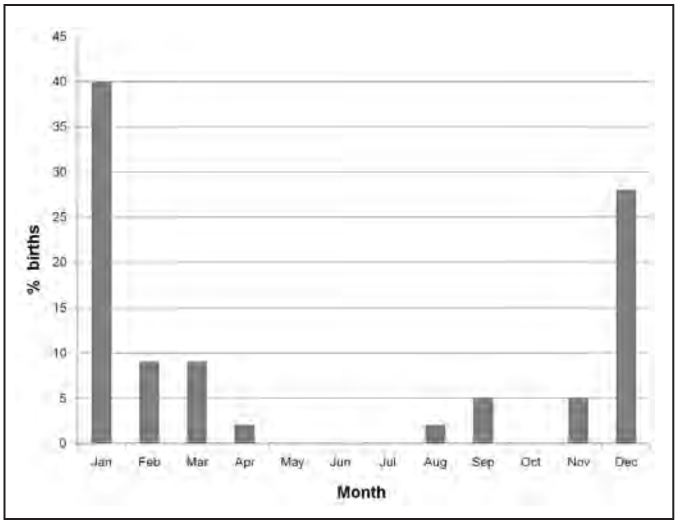

**Figure 3.** Birth seasonality in the European captive population of crowned sifaka (*Propithecus coronatus*) 1987 to 2011.

and January (Fig. 3). An exception to this were three births in August and September, all to the same female and in each case following the death of a previous baby in January or February; it is important to note that this was always the same female. The shortest interbirth interval was 219 days (7.2 months, following death of a baby), but most were approximately 12 months (range 9 to 14 months), and one female twice went two years without breeding (Table 3). In the wild, females usually have one baby every two years (Pochron *et al.* 2005 for Milne-Edwards' sifaka *Propithecus edwardsi*; J. Razafindramanana, pers. comm. and C. Pichon, pers. comm. for crowned sifaka). A shorter interbirth interval following the death of an infant has been observed in the wild for Milne-Edwards' sifaka (Pochron *et al.* 2005).

The age of the youngest captive-born male at the birth of his first offspring was 3 years, 7 months, and 4 days. The youngest female to have her first baby was 3 years, 2 months, 22 days. The age of the oldest female to have given birth is over 20 years; wild-born, her exact age is unknown. On the two occasions we could be sure of the dates of conception, gestation length was 169 and 170 days. Mating between sifakas (Fig. 4) is very rarely observed. Estrus is more readily observed, as the animals' behavior changes. They become more active; in particular, a lot of marking can be observed, with the male systematically covering the marks of the female (Fig. 5). Additionally, the male follows the female when she moves, and she becomes more aggressive with him. Estrus is usually observed from May to August, with most occurring in July. Observations of estrus in February occurred 20 days after a female lost her baby (death of the baby or removal to be hand-raised). Only one female had a baby after such a postpartum estrus. There are usually three to five estruses per

**Table 2.** Annual mortality rates, cumulative survivorship (Lx) and fertility (Mx) of captive crowned sifakas (*Propithecus coronatus*) by age and by sex.

| | Males | Females | Males | Females | Males | Females |
|---|---|---|---|---|---|---|
| Age | Mortality | Mortality | Lx | Lx | Mx | Mx |
| 0 | 0.38 | 0.49 | 1 | 1 | 0 | 0 |
| 1 | 0.13 | 0.14 | 0.62 | 0.51 | 0 | 0 |
| 2 | 0 | 0.17 | 0.54 | 0.44 | 0 | 0 |
| 3 | 0.07 | 0 | 0.54 | 0.36 | 0.04 | 0.09 |
| 4 | 0 | 0.15 | 0.50 | 0.36 | 0.22 | 0.17 |
| 5 | 0 | 0.2 | 0.50 | 0.31 | 0.06 | 0.12 |
| 6 | 0 | 0 | 0.50 | 0.25 | 0.2 | 0.3 |
| 7 | 0 | 0 | 0.50 | 0.25 | 0.15 | 0.1 |
| 8 | 0 | 0 | 0.50 | 0.25 | 0.25 | 0.4 |
| 9 | 0 | 0 | 0.50 | 0.25 | 0.25 | 0.39 |
| 10 | 0 | 0 | 0.50 | 0.25 | 0.16 | 0.42 |
| 11 | 0.11 | 0 | 0.50 | 0.25 | 0.23 | 0.34 |
| 12 | 0.14 | 0 | 0.45 | 0.25 | 0.24 | 0.3 |
| 13 | 0.21 | 0.2 | 0.38 | 0.25 | 0.12 | 0.22 |
| 14 | 0 | 0.24 | 0.30 | 0.20 | 0 | 0.43 |
| 15 | 0 | 0 | 0.30 | 0.15 | 0 | 0.25 |
| 16 | 0.5 | 0 | 0.30 | 0.15 | 0.38 | 0.25 |
| 17 | 0 | 0 | 0.15 | 0.15 | 0.5 | 0.25 |
| 18 | 0 | 0 | 0.15 | 0.15 | 0.5 | 0.25 |
| 19 | 0 | 0.25 | 0.15 | 0.15 | 0.5 | 0.14 |
| 20 | 0 | 0 | 0.15 | 0.11 | 0.5 | 0.17 |
| 21 | 0 | 0.37 | 0.15 | 0.11 | 0.5 | 0 |
| 22 | 0 | 1 | 0.15 | 0.07 | 0.5 | 0 |
| 23 | 0 | 1 | 0.15 | 0 | 0.5 | 0 |
| 24 | 0 | 1 | 0.15 | 0 | 0 | 0 |
| 25 | 1 | 1 | 0.15 | 0 | 0 | 0 |
| 26 | 1 | 1 | 0 | 0 | 0 | 0 |

**Table 3.** Breeding success rates of captive crowned sifaka females (including information on breeding pairs).

| **Pairs: Female Male (studbook no.)** | **N. of offspring** | **No. of offspring still alive after 3 days** | **No. of offspring still alive today** | **Management of the group** | **Age of female at the time of the first birth** | **Rearing of the first baby** | **Age of the female at the time of the introduction to a male** | **Interval between the introduction to a male and the first birth** | **Interbirth Interval** |
|---|---|---|---|---|---|---|---|---|---|
| **Daya (2)**<br>**Solofo (5)**<br>Pair established in May 1994 | 10 (5.4.1)<br>Breeding from 1994 to 2001 (no successful breeding from 2002 ) | 8<br>(1 stillborn,+1 abortion)<br>Mortality =20% | 5<br>Mortality = 37.5 | No specific management<br>Max size group = 8 | ? (wild-born female) | Yes | ? (wild-born female) | 8 months | 1year (very regular)<br>2 offspring born during the same year (January–December) |
| **Hadja (6)**<br>**Andry (7)**<br>Pair established in April 1995 | 4 (4.0)<br>Breeding from 1995 to 1998–(last breeding of the female in 1998) | 3 (1 stillborn)<br>Mortality = 25% | 1<br>Mortality = 66.6% | Andry isolated from the mother and her young during 2 months from the day of birth; used to kidnap baby | ? (wild-born female) | No (stillborn) | ? (wild-born female) | 9 months | 11 to 14 months |
| **Linoa (18)**<br>**Andry (7)**<br>Pair established in 2002 | 8 (7.1) | 5 (2 stillborn)<br>Mortality = 37.5% | 3<br>(Mortality = 62.5 %)<br>Current group composition : 4.1 | | 4 years | Yes | 2.5 years | 1 year 9 months | 9 to 13 months |
| **Vick (9)**<br>**Ulrick (12)**<br>Pair established in June 1999 | 10 (6.4)<br>Breeding from 1995 to 2008 (death of the female) | 5 (1 hand-reared animal)<br>Mortality = 50% | 3<br>Mortality= 70% | The females are very nervous at the time of birth and have to be isolated/ become less nervous with age | 6 years and 2 months | No | 4 years and 7 months. | 1 year 7months | 7–7.5 months if the baby does not survive<br>10 to 12 months |
| **Cixi (30)**<br>**Tao (17)**<br>Pair established in June 2006 | 2 (1.1)<br>Breeding from 1995 to 2008 (death of the female) | 1<br>Mortality = 50% | 0<br>Mortality=100% | | ~3 years | No | 2.5 years | 9 months | 10 months |
| **Holly (8)**<br>**Locky (10)**<br>air established in May 1998 | 10 (4.4.2)<br>Breeding from 1995 to 2009 (death of the male) | 5 (hand-reared animals)<br>(2 abortions) | 2 | All the young hand-reared.<br>Female has abnormal nipples | ? (Wild-born female) | No<br>(Abnormal nipples) | ? (Wild-born female) | 1 year 9 months | 1 year<br>(except 2 years without breeding and if we don't consider the 2 abortions 6 and 7 months after the death of a baby) |
| **Holly (8)**<br>**Minos (24)**<br>Pair established in September 2009 | 1 (0.1) | 1<br>(hand-reared animals) | 1<br>Current group composition : 2.2 | | | | | 1 year 4 months | |

reproductive season. Often the females are not very regular, with estruses separated by approximately one month, and lasting about ten days.

Body weights of adults in the captive crowned sifaka population range from 3.5 to 4.5 kg for males, and from 3.5 to 5.0 kg for females. Infant body weight at birth ranges from 67 to 116 g for males (mean 92.6 g) and from 70 to 105 g for females (mean 91.3 g).

**Figure 4.** Mating of a pair of captive crowned sifaka (*Propithecus coronatus*). Photograph by F.-G. Grandin, MNHN.

## Diet

In the wild, the crowned sifaka diet consists mainly of leaves, but fruits, flowers, vegetative buds and sometimes young stems are also eaten (Pichon *et al.* 2010). In the European captive population leaves are also an important part of the diet of the animals, mostly of false acacia *Robinia pseudoacacia*. They are given a mixture of vegetables, Mazuri® Leaf-eater Primate Diet pellets (www.mazuri.eu), some fruits and an in-house mix made with cereal, powdered milk and water.

## Social Organization

In the wild the crowned sifaka lives in groups of two to eight individuals (King *et al.* 2012; Pichon 2012; Rakotonirina *et al.* 2014), usually with only one breeding female (Pichon 2012; Rakotonirina *et al.* 2014; pers. obs.). In the European captive population, all the groups are composed of one breeding male and one breeding female and their offspring. When the first animals arrived, several attempts were made to keep more than one breeding male or breeding female in a group, but without success. They are very territorial, and adult animals of the same sex are very aggressive towards each other. The largest group size in captivity that we know of is eight. The females are dominant, coming to the food first and having priority of access. Some females are very aggressive towards males.

It is necessary to remove young females from their group at sexual maturity; at about 2.5 years old when they develop their first estrus. This is due to tension with the mother at this time. The change in behavior of the young females is obvious—they are more isolated from the rest of the group, give the impression of being unhappy, and are more distant with the keepers.

**Figure 5.** Scent-marking by a captive male crowned sifaka (*Propithecus coronatus*). Photograph by F.-G. Grandin, MNHN.

**Figure 6.** Part of the hand-rearing protocol for crowned sifaka (*Propithecus coronatus*) set up at Paris. Photograph by F.-G. Grandin, MNHN.

**Figure 7.** The Amboloando forest fragment, Dabolava, Madagascar. Photograph by F.-G. Grandin, MNHN.

Adult males seem to be more tolerant of their sons than the females are of their daughters. Indeed, the tension we observed between fathers and sons did not appear until the sons were about five years old. This tension appeared at the time of estrus, as in females. Only one young male was actively rejected by his father, at five years old. We did not observe fighting between him and his father, but one day the young male seemed very scared of his father. We heard a lot of "sifak" calls coming from him, and had to quickly remove him from the group.

## Management of the European Captive Population

The size of the European captive population of crowned sifaka has been declining since 2005, especially in the number of females (Fig. 1), resulting in the youngest proven breeding female in the current population being an elderly 11 years old. Three major factors can explain this recent decline: 1) the death from old age of the best breeding female in the population in 2005, one of the original wild-born founders; 2) an increase in transfers between institutions, especially in 2008 with the closing of the Parc Zoologique de Paris for renovation, that led to an increase in deaths due to digestive problems and infectious diseases; and 3) the difficulty of other members of the program to breed this species successfully and even sometimes to keep it, illustrated by a high mortality of newborns and even of adults, especially females.

To counter this third factor, newborns are now closely monitored, comparable to what is done at the Duke University Primate Center in the USA for Coquerel's sifaka (Haring 2009), and following a unique hand-rearing protocol set up at Paris in 2005. In this protocol the females are trained to allow the keepers to take their baby from them to conduct regular check-ups (Fig. 6). This protocol, which was first initiated for a wild-born female showing abnormal nipples that prevented her from feeding her babies, allowed for the hand-raising of several of her babies whilst keeping the mother and baby in contact.

The main issue in the management of this captive population is the lack of females. The sex ratio is clearly biased towards males: about three males for each female. The management of surplus males is problematic due to the instability of single-sex groups comprising adult males. Two adult males are successfully kept together with the help of Deslorelin implants, which inhibit testosterone production (previously used with male Coquerel's sifaka; D. Haring, pers. comm.). However, while the implants probably reduced the aggressiveness of the animals at the time of the contact, it is the age difference between them that was probably the most important factor in the success of this group. Even with the implants, it was impossible to add a third male of the same age as the older one to this group. Consequently, several males are currently kept without conspecifics but share enclosures with other lemur species, often bamboo lemurs *Hapalemur* spp. and ring-tailed lemurs *Lemur catta*.

## Conservation activities

Since 1998, several members of the EEP are actively involved in *in situ* conservation projects. The "Projet pilote bioculturel d'Antrema" concerns one of the largest populations of crowned sifaka in Madagascar. This project was initiated by the Parc Zoologique de Paris (Muséum national d'histoire naturelle) in 1998, and led, in 2000, to the creation of the "Station forestière à usage multiple d'Antrema". The first observations of crowned sifakas in mangroves were made in Antrema in the early days of the project (Gauthier *et al.* 1999). From 2008, another EEP member, Mulhouse Zoo, initiated a survey of crowned sifaka populations living in very degraded forests near Mahajanga (Boanamary), in collaboration with national partners Fanamby and Mahajanga University (P. Moisson and B. Lefaux, pers. comm.).

Since 2009, several EEP members support the "Dabolava project," which concerns the conservation of a group of seven crowned sifakas living in a fragment of forest at Dabolava, near Miandrivazo (Fig. 7; Razafindramanana and Rasamimanana 2010). The isolation of this site, and the discovery of additional small populations by the "Tsibahaka project" initiated and coordinated by The Aspinall Foundation (TAF 2009; King *et al.* 2012; Rakotonirina *et al.* 2014), led to the creation of a more global project of *ex situ* and *in situ* metapopulation management. Five members of the EEP (Cotswold Wildlife Park, Muséum de Besançon, Belfast Zoo, Parc Zoologique de Paris, and Port Lympne Wildlife Park through The Aspinall Foundation) and the SECAS (a French association close to Paris Zoo) are actively involved in this project. The *Association Européenne pour l'Etude et la Conservation des Lémuriens* (AEECL) opened a special account for the conservation of the crowned sifaka, which enabled the participation of public zoos in this project. The project "Conservation of the Crowned Sifaka," coordinated by Josia Razafindramanana, was awarded 17,801 Euros by the EAZA Madagascar Campaign fund in 2011.

The first technical meeting for the conservation of the crowned sifaka was primarily funded by EAZA. During this meeting, the captive population, which is an important part of the metapopulation conservation project, especially in the management of the most isolated groups living in very small fragments of forest, was identified as one of the priorities for the conservation of the crowned sifaka (MEF/GERP/TAF 2011). As part of the crowned sifaka metapopulation project, once the most isolated groups without a chance to survive in the wild have been identified, some of them should be included in the captive population. Initially these animals would stay in Madagascar in order to implement a captive breeding program *in situ*. Lemurs Park, the only zoo in Madagascar that has, for many years, successfully maintained this species in captivity, has been identified as the most appropriate place to establish this Malagasy captive population. This captive population will be managed by the EEP, with Lemurs Park becoming a member. The objective is to set up an international management regime of the captive population, and exchange animals between Europe and Madagascar to increase the global genetic diversity of the captive population. This should lead to the development of a sustainable captive population able to reinforce, in the future, wild populations if necessary, especially those that are isolated. The experience of the EEP will also help to arrange translocations of crowned sifakas between forest fragments that are included in the metapopulation conservation project. These animals will be individually identified and added to the European studbook that will evolve to a global data base for the project.

## Education Activities

Numerous educational events on the crowned sifaka are organized in Europe by members of the EEP. The primary objective is to collect funds for the conservation of the species, but zoos also contribute to informing people about the situation of the crowned sifaka in the wild. An educational project was developed in 2010 by the EEP in connection with the *in situ* metapopulation project. The aim is to encourage EEP members to support a joint educational project and to facilitate exchanges between Malagasy and European schools, but also between European schools. The project has three goals.

1. To create a teaching kit on the crowned sifaka. This tool, easy to move and to use, will help explain to Malagasy and European children what a sifaka is, where it lives, why it is threatened, and how and why to protect it.
2. To sponsor the crowned sifaka at Dabolava; funds for the conservation of the animals and for the publication of a comic on environmental education (created by Roots and Shoots), the first edition of which was tested with Malagasy children in 2011 (J. Razafindramanana, pers. comm.).
3. To collect French books, various school materials, and donate posters on the crowned sifaka for Malagasy schools to contribute to improving education (Fig. 8).

**Figure 8.** Poster about crowned sifaka (*Propithecus coronatus*) for the Davolava primary school, Madagascar. Photograph by F.-G. Grandin, MNHN.

## Conclusion

The EEP captive population plays an important role in the conservation of the crowned sifaka. Despite the problems encountered in the management of this breeding program, the 25 years of captive management of the crowned sifaka have led to better knowledge of the species, including descriptions of many behaviors that would be difficult to observe in the wild—most especially concerning the reproduction of *P. coronatus* at Parc Zoologique de Paris—and a better understanding of the needs of the species and improvement of captive husbandry. The involvement of several members of the EEP in *in situ* projects, especially their fundraising activities, led to the proposition of the metapopulation conservation project in which the EEP will help with the management of the most isolated groups of crowned sifakas, including the implementation of a sustainable captive population. Finally, the educational activities conducted by the EEP and/or its members improve awareness of the species and contribute to its protection.

## Acknowledgments

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# Diet of the Ashy Red Colobus (*Piliocolobus tephrosceles*) and Crop-Raiding in a Forest-Farm Mosaic, Mbuzi, Rukwa Region, Tanzania

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**Abstract:** The Ashy red colobus monkey (*Piliocolobus tephrosceles*) was recently discovered in the Mbuzi Forest. Since then its forests have been degraded, fragmented and converted into farmland. In this study I documented the diet, including cultivated crops, of four groups in the Mbuzi forest-farm mosaic during two months in the crop-growing season, July–August 2011. Each group was followed for nine days; 36 days overall. It was not possible to extend the study in subsequent years because the forest was so fragmented that the monkeys were no longer staying in some patches. The monkeys fed mostly on wild plants. Crop-raiding was limited to beans, and occurred in the evenings when the farmers had left the fields. Extreme fragmentation, degradation and widespread forest conversion into farmland have drastically reduced the abundance of food trees; and it is likely that this has resulted in their crop-raiding. They are persecuted for this behavior, and retaliatory killing by farmers is probably contributing to their decline in the Mbuzi Forest. The conservation of intact montane forests on the Ufipa Plateau is crucial and urgent. Measures must include conservation education, community involvement and improved law enforcement, as well as provisions for local communities to reduce the destruction of the remaining forest patches.

**Key Words:** Ashy red colobus, *Piliocolobus tephrosceles*, *Procolobus rufomitratus tephrosceles*, diet, bean-crop raiding, Mbuzi Forest

## Introduction

Folivorous monkeys such as the Ashy red colobus, *Piliocolobus tephrosceles* (Elliot, 1907)[1], select the most nutritive and easily digestible items, rich in proteins, such as young leaves and leaf buds (Chapman and Chapman 2002). They also eat other plant parts and arthropods to supplement their diet. Seasonal food-switching is common among primates as a strategy to meet their dietary requirements (Li *et al.* 2010). Differences in habitat quality also affect habitat use by primates; for instance, *P. tephrosceles* spends more time in patches with a high density and diversity of food trees than patches with a low food tree density and diversity (Kibaja 2012). The carrying capacity of their habitats is compromised if it is unscrupulously degraded by human activities.

*Piliocolobus tephrosceles* is categorized as 'Endangered' on the IUCN Red List (Struhsaker 2008), the only viable population possibly being in Kibale, with at least 17,000 individuals (Struhsaker 2005). There has, however, been a decline in population and group sizes in past years (Chapman *et al.* 2007) due to, among other factors, predation by chimpanzees (*Pan troglodytes*) (Watts and Mitani 2002; Fourier *et al.* 2008; Struhsaker, 2008). On the Ufipa Plateau (Mbizi and Mbuzi forests) where there are no chimpanzees the monkeys are prone to extinction due to other forces. The human activities degrading and insularizing the forest have been reported by Davenport *et al.* (2007); and they continue to worsen in the Mbuzi Forest, which is gradually being converted into farmland. Such habitat alterations have negative effects on the diet and feeding patterns of the monkeys. Human-grown foods also affect the monkey's dietary preferences. Tesfaye *et al*. (2013) noted that Boutourlini's blue monkeys (*Cercopithecus mitis boutourlinii*) raided crops of farms surrounding forest fragments but not those adjoining larger intact forests. While some primates, notably frugivores, can in some circumstances co-exist with humans, folivorous

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[1] Following Groves (2007). Classified as *Procolobus rufomitratus tephrosceles* in the IUCN Red List (Struhsaker 2008, 2010).

monkeys have more difficulty. Assessment of the monkeys' diets in these vulnerable habitats and surrounding agro-ecosystems is paramount.

Here I present my preliminary findings on the wild and cultivated foods eaten by Ashy red colobus monkeys in extremely degraded habitats. The results are a wake-up call for primatologists and conservationists to forestall the likely impacts of human activities to habitats of isolated vulnerable populations of primates in unprotected areas such as the Mbuzi Forest.

## Methods

### *Study site*

The study was conducted in the Mbuzi Forest in the Rukwa Region, Tanzania (Fig. 1). The forest is on the eastern ridge of the Ufipa Plateau in Nkasi District, northeast of Chala and 54 km northwest of Mbizi Forest (Davenport *et al.* 2007). The Ufipa Plateau covers an area of 7,249.4 km². It is an uplifted highland lying between the wings of the Albertine rift valley, east of Lake Tanganyika, and the Rukwa valley. The soils are ferralitic. Elevations range from 1,000 to 2,661 m above sea level, and annual rainfall is 800–1,200 mm. The plateau is an important agro-economic zone, supplying the marketed surplus of agricultural produce of the region (Anonymous 1998). The high population growth and concentration of people in the area have intensified land-use (Anonymous 1998).

The Mbizi Forest is protected as a forest reserve, but the Mbuzi Forest is not. The Mbuzi Forest is threatened with degradation, resulting from various forms of uncontrolled forest use (Davenport *et al.* 2007). It lies between 1,990 and 2,122 m above sea level and, according to Davenport *et al.* (2007), the forest covers about 611 ha. The area is now probably considerably smaller due to ongoing fragmentation and conversion into cultivated land in recent years.

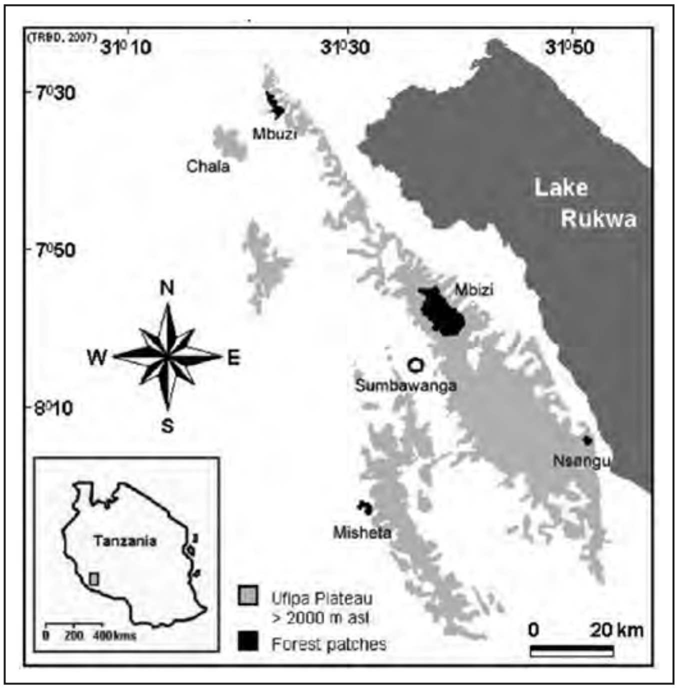

**Figure 1.** Mbuzi Forest on the Ufipa Plateau, Rukwa Region. From Davenport *et al.* (2007).

The Mbuzi Forest has been segmented into several forest patches. In this study, a forest fragment refers to a forest patch that has been broken from the once continuous area of the forest as a result of clearing for cultivation. I surveyed all fragments and only four were occupied by red colobus, each having a single group (G1, G2, G3 and G4): A (7º30'57.85097"S, 31º22'46.53323"E), B (7º30'30.76018"S, 31º22'42.39630"E), C (7º30'9.33958"S, 31º22'35.32957"E), and D (7º30'43.99333"S, 31º23'24.51921"E) (Fig. 2).

### *Feeding data collection and analysis*

Each of the four groups was followed for nine days, making a total of 36 days for the four groups inhabiting Mbuzi Forest (Fig. 2). The study was conducted during the crop-growing season from July to August 2011. It was not possible to extend the study in other years because the forest was so fragmented that the monkeys were fleeing some forest patches. I recorded the activities of the groups when following them, using an instantaneous scan sampling protocol (Altmann 1974), recording activities during five-minute scans at 15-minute intervals (Martin and Bateson 1993; Kitegile 2006). In each scan sample, I noted the activities of all visible monkeys. If feeding, the food item, plant part and plant species were identified. After each scan, I recorded my location with a Global Positioning System (GPS), and noted also the habitat type, time spent in a habitat, group size and weather conditions.

To estimate the relative importance of each habitat type, I summed the total feeding records (the sum of all the daily feeding records) for each food item in each. The Chi-square test was used to test the significance of variation in frequency of feeding records for the seeds of cultivated beans and items from wild species eaten in farms, and of feeding records of wild food items between forests and farms.

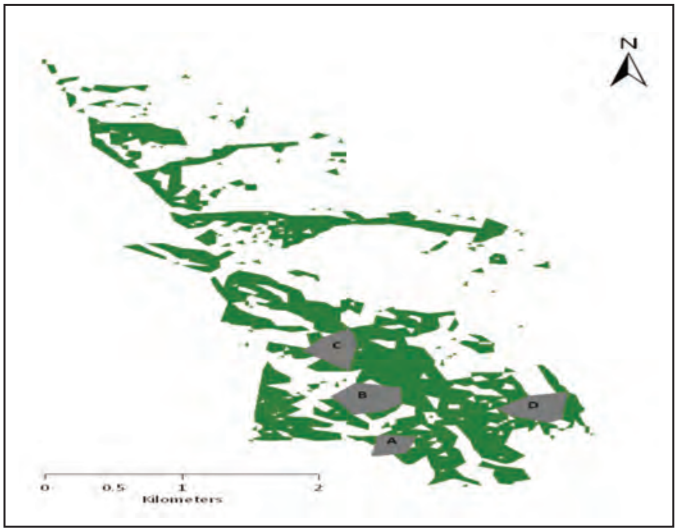

**Figure 2.** Locations of the four colobus groups in the forest fragments A–D, as shown by shaded polygons, in Mbuzi Forest, Tanzania.

**Table 1.** Frequency of parts eaten by four groups (G1–G4) of *Piliocolobus tephrosceles* in forest fragments (A-D) in a forest-farm mosaic, Mbuzi, Tanzania.

| | | **Groups (forest fragments)** | | | | |
|---|---|---|---|---|---|---|
| | **Food items** | **G1(A)** | **G2( B)** | **G3 (C)** | **G4 ( D)** | **Total** |
| **Wild plant foods** | Leaves | 256 | 526 | 555 | 513 | 1850 |
| | Leaf buds | 199 | 94 | 63 | 18 | 374 |
| | Bark | 4 | 1 | 1 | 34 | 40 |
| | Shoots | 1 | 4 | 8 | 0 | 13 |
| | Petioles & cork | 0 | 0 | 8 | 5 | 13 |
| | Dry twigs | 0 | 0 | 0 | 12 | 12 |
| | Flowers & fruits | 2 | 0 | 1 | 0 | 3 |
| | Lichens | 0 | 2 | 33 | 39 | 74 |
| **Bean** | **Seeds** | **36** | **2** | **0** | **0** | **38** |
| | **Total** | 498 | 629 | 669 | 621 | 2417 |

*Botanical data collection and analyses*

I sampled the vegetation in the forest patches habitually used by the Ashy red colobus monkeys. Reconnaissance surveys revealed that the monkeys in the Mbuzi Forest feed on a variety of plants, including trees, shrubs, and lianas, and sometimes even herbs on the ground. The botanical data for trees are considered here for the computation of food selection ratios. Vegetation sampling involved two random plots in each habitat type (open canopy, closed canopy forest and forest edge) in each of the four forest fragments, totaling 22 plots in the forest fragments and 8 plots in the farms. Sampling involved the following quadrat dimensions with modification from Mligo *et al.* (2009) (a) 25 × 20 m quadrats for trees; covering 1.1 ha (22 plots) in the forests and 0.4 ha (8 plots) in the farms (b) 5 × 2 m quadrats nested in the bigger quadrat for shrubs and (c) 1 × 1 m quadrat nested in the 5 × 2 m quadrats for the herbaceous layer (i.e. forbs, seedlings and grasses). The following were recorded in each quadrat: scientific name of the plant, the girth of the trees at breast height, or above the buttress if large fig trees (*Ficus*), using a tape measure, and an estimate of cover for herbs in 1 × 1 m plots.

Tree density was determined by recording the number of trees in a known area and dividing it by the area from which they were sampled, later converted into number of trees per hectare: Density of species (D) = number of trees of each species / total area sampled (ha). The basal area was calculated by using the formula: $BA = \pi (DBH / 2)^2$, where BA = basal area, $\pi = 3.14$; and DBH = diameter of a tree at breast height. The basal area was used to compute the selection ratios of food trees in the forests and farms. The formula used was as follows: $SR = \%f_n / \%BA_n$, where SR = selection ratio of a food tree species n; $\%f_n$ = percentage of tree feeding records of species n in the study period; $\%BA_n$ = percentage basal area (BA) for tree species n in a given habitat. Unpaired two-sample t test (computed in PAST: Paleontological Statistics Version 2.17 Software by Hammer 2012) was used to test the significance of the differences in density and basal area of trees in the diet between forests and farms.

**Table 2.** Feeding records of plant food items in forests and farms, Mbuzi, Tanzania.

| **Food items** | **Forests** | | **Farms** | | **Total frequency** |
|---|---|---|---|---|---|
| | **F** | **%F** | **F** | **%F** | |
| Leaves | 1801 | 77.7 | 49 | 49.5 | 1,850 |
| Leaf buds | 368 | 15.9 | 6 | 6.1 | 374 |
| Bark | 40 | 1.7 | 0 | 0 | 40 |
| **Bean seeds** | **-** | **-** | **38** | **38.4** | **38** |
| Shoots | 12 | 0.5 | 1 | 1.0 | 13 |
| Petioles and cork | 13 | 0.5 | - | - | 13 |
| Dry twigs | 7 | 0.3 | 5 | 5.1 | 12 |
| Flowers and fruits | 3 | 0.1 | - | - | 3 |
| Lichens | 74 | 3.2 | - | - | 74 |
| **Total** | **2318** | **100** | **99** | **100** | **2,417** |

## Results

Of 2,417 feeding records, 2,379 (98.4%) were of wild foods. Cultivated bean seeds amounted to 38 records (1.6%) in the forest-farm mosaic. Consumption of wild food items was higher in forests (97.4%, n = 2318) than in farms (2.6%; n = 61). In the farms, the monkeys ate more wild food items (61.6%, n = 61) than cultivated bean seeds (38.4% n = 38) ($\chi^2$ = 5.343, df = 1; P = 0.021). The percentage frequency of feeding records between wild plant items (not cultivated beans) and bean seeds differed significantly among the monkey groups G1–G4 (Contingency table: $\chi^2$ = 129.970; P < 0.0001). Only groups G1 and G2 ate bean seeds (Table 1).

Leaves comprised the majority of the diet in both forests and farms (Table 2). Among the cultivated crops, only beans (*Phaseolus*) were eaten, complementing the wild plant foods. The monkeys ate fresh beans (seeds) and discarded the pods. They would raid the bean crops in the early morning and (mostly) late evenings at around 1700 h–1900 h (Fig. 3) when peasant farmers were not around. Whereas, the farmers guarded the bean plantations, farms with other crops were

**Table 3.** Feeding records of food plants in the forest fragments and fields, Mbuzi, Tanzania.

| Family | Food plant | Author(s) | Forests | | Farms | | Parts eaten |
|---|---|---|---|---|---|---|---|
| | | | F | %F | F | %F | |
| Chrysobalanaceae | [a]*Parinari excelsa* | Sabine | 990 | 44.0 | 43 | 43.9 | YL, LB |
| Mimosaceae | [a]*Newtonia buchananii* | Baker | 335 | 14.9 | 6 | 6.1 | YL, LB |
| Moraceae | [a]*Ficus thonningii* | Blume | 299 | 13.3 | | | YL, LB |
| Celastraceae | [a]*Catha edulis* | (Vahl) Forssk ex Endl | 2 | 0.1 | | | B |
| Sapotaceae | [a]*Chrysophyllum gorungosanum* | Engl. | 204 | 9.1 | | | YL, LB |
| Convolvulaceae | [c]*Ipomea ficifolia* | Lindl. | 68 | 3.0 | 1 | 1.0 | YL. LS |
| Mimosaceae | [a]*Albizia gummifera* | A. Sm | 55 | 2.4 | | | YL, LS |
| **Fabaceae** | [c]Phaseolus **sp.** | **(Herb. Linn)** | **0** | **0.0** | **39** | **39.8** | **SD** |
| Myrsinaceae | [a]*Rapanea melanophloeos* | (L.) Mez | 34 | 1.5 | | | B |
| Myrtaceae | [a]*Syzygium guineense* | Wall | 34 | 1.5 | | | YL |
| Parmeliaceae | [e]*Parmotrema* sp. | | 27 | 1.2 | | | |
| Euphorbiaceae | [a]*Croton megalocarpus* | Del. | 24 | 1.1 | | | YL, B |
| Moraceae | [a]*Ficus natalensis* | Hochst. | 22 | 1.0 | | | LB |
| Araliaceae | [a]*Polyscias fulva* | (Hiern) Harms | 19 | 0.8 | | | LS, ML |
| Ebenaceae | [a]*Euclea divinorum* | (Hiern) | 18 | 0.8 | | | B, YL |
| Compositae | [c]*Crassocephalum vitellinum* | (Benth.) S. Moore | 18 | 0.8 | | | YL |
| Acanthaceae | [c]*Brillantaisia owariensis* | (P. Beauv) | 12 | 0.5 | | | YL |
| Araliaceae | [a]*Schefflera goetzenii* | (Harms) | 11 | 0.5 | | | LB |
| Boraginaceae | [a]*Ehretia amoena* | Klotzsch | 11 | 0.5 | | | YL |
| Agavaceae | [a]*Dracaena steudneri* | (Schweinf. ex Engl.) | 3 | 0.1 | 7 | 7.1 | L, YS |
| Cucurbitaceae | [c]*Momordica foetida* | Schumacher | 9 | 0.4 | 1 | 1.0 | YL |
| Parmeliaceae | [e]*Usnea* sp. | | 9 | 0.4 | | | |
| Melianthaceae | [a]*Bersama abyssinica* | Fresen. | 5 | 0.2 | | | YL |
| Solanaceae | [c]*Solanum terminale* | Forssk. | 5 | 0.2 | | | YL |
| Rubiaceae | [a]*Tarenna graveolens* | (S.moore) Bremek | 4 | 0.2 | | | B, YL |
| Compositae | [b]*Vernonia amygdalina* | Del. | 4 | 0.2 | | | YL |
| | [d]Unidentified liana | | 4 | 0.2 | | | L |
| Rubiaceae | [a]*Psychotria goetzei* | (K. Schum) | 3 | 0.1 | | | LB |
| Stilbaceae | [a]*Nuxia congesta* | R. Br. Ex Fresen | 3 | 0.1 | | | FR, Fl |
| Proteaceae | [a]*Faurea saligna* | Harv. | 3 | 0.1 | | | B |
| Anacardiaceae | [b]*Rhus natalensis* | Bemh. Ex Krauss | 2 | 0.1 | | | YL |
| Phytolaccaceae | [b]*Phytolacca dodecandra* | Vitten | 2 | 0.1 | | | YL, LB |
| Cacastraceae | [a]*Elaeodendron buchananii* | (Loes.) Loes. | 2 | 0.1 | | | YL |
| Meliaceae | [a]*Lepidotrichilia volkensii* | (Gürke) Leroy | 2 | 0.1 | | | YL |
| | [c]Unidentified herb | | 2 | 0.1 | | | L |
| Myrsinaceae | [a]*Maesa lanceolata* | Forssk | 1 | 0.04 | | | YL |
| Rubiaceae | [a]*Hallea rubrostipulata* | (Schumann) Havil | 1 | 0.04 | | | YL |
| Rutaceae | [a]*Clausena anisata* | (Wild.) Hook.f.ex Benth | 1 | 0.04 | | | YL |
| Icacinaceae | [a]*Apodytes dimidiata* | C. A. Sm. | 1 | 0.04 | | | YL |
| Mimosaceae | [a]*Acacia tortilis* | Del. | | | 1 | 1.0 | YL |
| | Unidentified parasitic plant | | 1 | 0.04 | | | |

YL = Young leaves; ML= Mature leaves; LB= Leaf buds; LS= Leaf stalks; YS = Young shoots; L = Leaves; FR = Fruits; Fl = Flowers; SD = Seeds; B = Barks; F = Feeding records, %F = % feeding. Superscript a = tree; b = shrub; c = herb; d = liana; e = lichen.

**Table 4.** Overall selection ratios for trees in the forest and farms in Mbuzi, Tanzania.

| Food plant | Forests | | | | Farms | | | |
|---|---|---|---|---|---|---|---|---|
| | F | %F | %BA | SR | F | %F | %BA | SR |
| *Parinari excelsa* | 990 | 47.5 | 45.5 | 1.0 | 43 | 75.4 | 45.1 | 1.7 |
| *Newtonia buchananii* | 335 | 16.1 | 9.5 | 1.7 | 6 | 10.5 | 6.8 | 1.5 |
| *Ficus thonningii* | 299 | 14.3 | 1.4 | 10.2 | | | | |
| *Catha edulis* | 2 | 0.1 | 1.4 | 0.1 | | | | |
| *Chrysophyllum gorungosanum* | 204 | 9.8 | 5.3 | 1.8 | | | | |
| *Albizia gummifera* | 55 | 2.6 | 0.8 | 3.3 | | | | |
| *Rapanea melanophloeos* | 34 | 1.6 | 2.3 | 0.7 | | | | |
| *Syzygium guineense* | 34 | 1.6 | 5.2 | 0.3 | | | | |
| *Croton megalocarpus* | 24 | 1.2 | 13.4 | 0.1 | | | | |
| *Ficus natalensis* | 22 | 1.1 | 0.2 | 5.3 | | | | |
| *Polyscias fulva* | 19 | 0.9 | | | | | | |
| *Euclea divinorum* | 18 | 0.9 | 0.9 | 1.0 | | | | |
| *Schefflera goetzenii* | 11 | 0.5 | | | | | | |
| *Ehretia amoena* | 11 | 0.5 | 2.6 | 0.2 | | | | |
| *Dracaena steudneri* | 3 | 0.1 | 0.3 | 0.5 | 7 | 12.3 | 4.3 | 2.9 |
| *Bersama abyssinica* | 5 | 0.2 | 3.5 | 0.1 | | | | |
| *Tarenna graveolens* | 4 | 0.2 | | | | | | |
| *Psychotria goetzei* | 3 | 0.1 | 2.3 | 0.1 | | | | |
| *Nuxia congesta* | 3 | 0.1 | 3.5 | 0.0 | | | | |
| *Faurea saligna* | 3 | 0.1 | 0.1 | 1.4 | | | | |
| *Elaeodendron buchananii* | 2 | 0.1 | | | | | | |
| *Lepidotrichilia volkensii* | 2 | 0.1 | 0.2 | 0.5 | | | | |
| *Maesa lanceolata* | 1 | 0.05 | 1.7 | 0.03 | | | | |
| *Hallea rubrostipulata* | 1 | 0.05 | | | | | | |
| *Clausena anisata* | 1 | 0.05 | | | | | | |
| *Acacia tortilis* | 0 | 0.0 | | | 1 | 1.8 | 1.34 | 1.3 |

F = Feeding records, %F = % feeding records; BA = Basal area of food tree n; SR = Selection ratio of food tree n.

**Table 5.** Density and basal area of food trees in forest fragments and farms, Mbuzi, Tanzania.

| Forest fragments | Farms | Unpaired two-sample t test |
|---|---|---|
| 447 trees/ha | 123 trees/ha | t = 4.224; df = 28; P = 0.013 |
| 22 trees/plot | 6 trees/plot | t = 2.997; df =28; P = 0.040 |
| 28.59 m²/ha | 10.24 m²/ha | t = 4.200; df = 28; P = 0.014 |

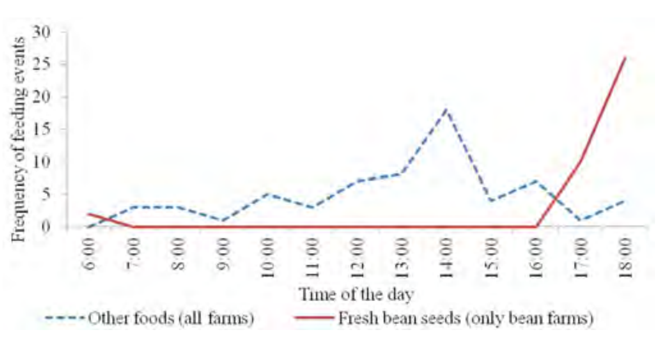

**Figure 3.** Bean crop raiding and other foods eaten with respect to times of the day (bean seeds were eaten only in bean farms). Other foods = food items other than bean seeds eaten in all farms with different crops such as maize, wheat, beans and sorghum, Mbuzi, Tanzania.

rarely guarded, and in those farms monkeys were seen to forage for wild foods and rest in the trees.

The monkeys were seen eating items of 36 identified higher plants, along with two lichens, and some herbs, a liana and a parasitic plant that we were unable to identify. The difference in feeding frequencies on wild species and the bean crop (*Phaseolus*) in the farms was significant ($\chi^2 = 4.082$; df = 1; P = 0.043). The most frequently eaten items in both forests and farmland were the young leaves and leaf buds of *Parinari excelsa* (Table 3). Despite having the most feeding records, *P. excelsa* trees had low selection ratios, possibly because of their highest basal area in both forests and farms. *Ficus thonningii, F. natalensis* and *Albizia gummifera* were mostly selected relative to their abundances in the forests, whereas *Dracaena steudneri* was selected more than expected from its abundance in farms (Table 4). The density and basal area of the trees providing food for monkeys were greater in the forest than in the farms (around the fields) (Table 5).

## Discussion

Young leaves and leaf buds were predominant in the diet of the Ashy red colobus in the forest and the farmland. They spent more time feeding in the forest than the farmland, associated with a smaller basal area and lower density of wild food trees in farmland (Table 5). Some of the important food trees (for example, *P. excelsa*) have been reported as staple food plants for *P. tephrosceles* in Kibale National Park, Uganda (Isbell 2012). Some species in the diet had high selection ratios in the forest and were not found in the farms. Some tree species with a high selection ratio in farms (for example, *D. steudneri*) had low selection ratios in the forest. This indicates that they select certain food plant species based on accessibility, availability, abundance and nutritional content. Some species that were selected by monkeys were not abundant and some which were abundant scored low selection ratios despite their having a high number of feeding records. Mturi (1991) regarded the less eaten plant species to be ‘unpreferred’ when their selection ratios were less than one (1.0). However, even though ‘unpreferred’ they may still make up a significant portion of the diet. Mturi (1991) provided two explanations for this: (1) plant species exploited less than expected had selection ratios of less than one (1.0) but made up a significant portion of the diet just because they were abundant (for example *P. excelsa*); (2) they might not be ‘unpreferred’, but they were eaten less than expected from their abundance because they were highly abundant and there is a limit to the extent they could be eaten by the monkeys, either due simply to quantity or because of the need to diversify the diet for nutritional reasons. A number of studies have indicated that the plant species that are highly selected despite their low abundance, have a high protein content and low levels of secondary compounds (McKey and Gartlan 1981; Mturi 1991; Fashing *et al.* 2007; Chapman and Chapman 2002). Despite the observed variation in selection ratios of food trees, the conservation of all plant species in the forest is of paramount importance as it is possible that plants eaten less would contribute significantly to the diet of the monkeys for nutritional balance. The red colobus monkeys would occasionally go to the ground to feed on herbaceous vegetation and beans in the forest and farms, respectively.

**Figure 4.** Guides showing a skin of red colobus monkey killed on a bean farm, Mbuzi, Tanzania.

Crop raiding by the colobus monkeys was infrequent. Sympatric guenons such as the blue monkey (*Cercopithecus mitis*) also raid crops, but blame was usually directed towards the colobus monkeys, probably because the farmers were asked to preserve the forests as habitats specifically for the Endangered red colobus monkeys. Blue monkeys did not stay in the fragments surrounded by farms; they would move far off after feeding, while the red colobus monkeys would stay in the fragments, only raiding crops if there were no people around. The monkeys ate the beans and discarded the pods. Group 1 raided bean crops more than others; fragment A was surrounded by bean farms, whereas farms around the other fragments also cultivated maize, wheat and sorghum. Farmers cultivating beans guarded their crops. Those growing other crops rarely did so, and the monkeys could be seen foraging and resting in the trees on these farms near the edge of the forest.

The colobus monkeys raided bean crops in the evenings around 1700 h–1900 h (Fig. 3) after the farmers had left to go home (see also Strum 2010). The farmers tend to kill the monkeys with the help of dogs because of this behavior. During the preliminary surveys in July 2011, we found a skin of an adult red colobus placed in a tree near the forest to intimidate other monkeys not to raid crops (Fig. 4). Retaliatory killing of monkeys by farmers is believed to be one of the factors leading to the decline of red colobus in the Mbuzi Forest, and Struhsaker (2005) listed hunting as a major threat facing red colobus monkeys in their natural habitats. Exposure of colobus monkeys to parasites and pathogens at the forest-farm interface is possible, as reported by Chapman *et al.* (2006) in Kibale National Park.

Tentative explanations have been offered as to why *P. tephrosceles* feed on fresh bean seeds. Seeds are rich in fats, proteins, and minerals such as phosphorus, which are limiting to vegetarians (Janson and Chapman 1999). It is here argued that the monkeys feed on fresh beans owing to their digestibility, for supplementary protein, or because of reduced food availability due to ongoing forest fragmentation, degradation and destruction. All the four fragments occupied by the monkeys are extremely fragmented and degraded, as previously reported by Davenport *et al.* (2007). Although degradation was not quantified in this study, it is possible that it has drastically reduced the numbers of food trees for monkeys. Young leaves and flowers of the beans were also eaten by the monkeys.

Fragmentation processes continue to increasingly divide and isolate the forest fragments. Forest clearance is evidently aggravated by a lack of clarity as to forest ownership, creating conflicts among the farmers. The local government authority categorically orders that forests, which farmers believe to be their property, be preserved, in particular for the Endangered Ashy red colobus. Protracted disputes regarding ownership and infrequent patrols by the District Forestry and Wildlife Division result in the forests being divided up amongst the villagers. Other common challenges reported by Oates (2013) are evident in the Mbuzi Forest. It is possible that in many areas nothing or very little remains to support the monkeys; probably the reason for their decline in the Mbuzi Forest on the Ufipa Plateau of the Rukwa Region.

The continued existence of *P. tephrosceles* in the Mbuzi Forest will depend on the effective conservation of their remaining forest patches, addressing the causes of their deterioration and allowing them to recover. Conservation interventions should consider community conservation measures, the provision of adequate funding to local governments for effective law enforcement, and the settlement of forest ownership conflicts, and conservation education, as suggested by Oates (2013).

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# Primate Conservation in the Rangeland Agroecosystem of Laikipia County, Central Kenya

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**Abstract:** Maintenance of the diversity of primates depends not only on the conservation of protected areas, but also on the conservation of areas that lack formal protection and are occupied by people, crops, and/or livestock. Livestock rangelands, when well-managed, can support viable populations of primates. This article describes (1) the primate community in the rangeland agroecosystem of Laikipia County, central Kenya, (2) how primates use this agroecosystem, (3) the importance of this agroecosystem to the primates of Laikipia, and (4) the threats to these primates. Patas monkeys *Erythrocebus patas*, olive baboons *Papio anubis*, vervet monkeys *Chlorocebus pygerythrus*, and northern lesser galagos *Galago senegalensis* in the Laikipia rangeland agroecosystem benefit from man-made perennial water sources, habitat protection, reduced large predator densities, and an array of research and conservation activities. The level of conflict between humans and non-human primates in this rangeland agroecosystem is low relative to that in neighboring cropland agroecosystems. The main threats are habitat fragmentation, degradation and loss, and the decline of perennial water sources. Hunting is not a serious threat to primates in Laikipia. *Erythrocebus patas* is the most threatened primate in Laikipia and the one least tolerant of humans and habitat degradation and loss. Habitat conservation in Laikipia should focus on water-associated vegetation types and the adjacent whistling thorn *Acacia drepanolobium* woodlands, particularly along the Ewaso N'yiro River and its major tributaries.

**Key Words**: agroecosystem, conservation, cropland, Kenya, Laikipia County, primate, rangeland

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## Introduction

Africa supports a high diversity of primates (Groves 2001; Grubb *et al.* 2003), with 25 genera and 94 species (Butynski *et al*. 2013). The survival of many of Africa's primate species and subspecies is, however, under threat; the human population of Africa continues to double about every 20 years. There is no indication that the growth rate of Africa's human population (now about 3% per year), or the associated increasing demand for natural resources, will decline any time soon. The continent's current population of about 1 billion people is projected to rise to between 3.1 and 5.7 billion people (median projection of 4.2 billion) by the end of this century (Gerland *et al.* 2014).

The rising demand for natural resources in Africa has spear-headed increases in the hunting of primates for meat, and in the rates of degradation, loss and fragmentation of primate habitats, primarily through logging and conversion to agriculture (including the raising of livestock). These activities have greatly impacted most of Africa's primate taxa, leading to reduced numbers and geographic distributions and, thereby, to an increase in the number of threatened primate taxa (Butynski 2001; Chapman *et al.* 2006; Oates 2011; De Jong and Butynski 2012; Butynski and De Jong in press). Importantly, however, some of the land used for agriculture, including livestock production, can be of value to primate conservation (Estrada *et al.* 2012).

The persistence of biodiversity, including primates, depends not only on the conservation of official protected areas, but also on the conservation of vast tracts of land that lack formal protection, are privately or communally owned, and are occupied by people and their crops and/or livestock (Hutton *et al.* 2005; Didier *et al.* 2011; Georgiadis 2011b; Kinnaird and O'Brien 2012). Agroecosystems are ecosystems in which indigenous plants and animals are partially or completely replaced with crops and/or livestock (Altieri 2003; Estrada *et al.* 2012). The literature is replete with examples of primates of many taxa living, if not thriving, in agricultural matrices and in crop plantations (for example, Salafsky 1993; Michon and de Foresta 1995; McCann *et al.* 2003; Medhi *et al.* 2004; Raboy *et al.* 2004; Somarriba *et al.* 2004; De Jong *et al.* 2008; Schwitzer *et al.* 2011; Estrada *et al.* 2012).

The importance of agroecosystems to primate conservation has been rarely assessed for Africa. This article describes (1) the primate community in the rangeland agroecosystem of Laikipia County, central Kenya, (2) how primates use this agroecosystem, (3) the importance of this agroecosystem to the primates of Laikipia, and (4) the threats to these primates. In addition, recommendations are made for four activities that are expected to enhance the long-term conservation of Laikipia's primate community.

## Description of Laikipia County, Kenya

Laikipia County (*c.* 9,700 km²; Figs. 1 and 2) is demarcated by Mount Kenya (5,200 m asl) to the east and south-east, Aberdares Range (4,000 m asl) to the south and south-west, Eastern (Gregory) Rift Valley (*c.* 970 m asl) to the west, Karisia Hills (2,580 m asl) to the north-west, Mathews Range (2,688 m asl) to the north, and Samburu National Reserve (*c.* 900 m asl) to the north-east.

Through Laikipia County (hereafter referred to as 'Laikipia') there is considerable variation in geography, altitude, rainfall, soil, flora, fauna, human population density, and land use (Georgiadis 2011a; LWF 2011, 2013). These environmental variables generally change spatially through gradual transition, but sometimes the change is abrupt. Laikipia ranges in altitude from 1,260 m (Mukutan Gorge) to 2,400 m (Enghelesha Hill). Much of Laikipia is covered by the Laikipia Plateau (*c.* 1,600–2,400 m asl), an area composed of a mix of flat ground (mostly), undulating plains, rolling hills, steep hills (some with extensive erosion gullies), and scattered, often steep, granitic inselbergs (or "kopjes"). There are several small perennial rivers—the largest being the Ewaso N'yiro—and many seasonally dry stream channels and gullies, some of considerable size.

Mean annual rainfall ranges from *c.* 40 cm in the north to *c.* 120 cm in the south-west (LWF 2013). Mean annual temperature ranges from 16ºC to 26ºC (CAS 2013). The primary vegetation types are grassland, bushland, woodland, and, on the higher ground, dry forest. Dry forest is typically dominated by pencil cedar *Juniperus procera* (Cupressaceae), wild olive *Olea europaea* (Oleaceae), podo *Afrocarpus gracilior* (Podocarpaceae), euclea *Euclea divinorum* (Ebenaceae), acokanthera *Acokanthera schimperi* (Apocynaceae), and croton *Croton megalocarpus* (Euphorbiaceae). Riparian forest is a scarce, but biologically important, vegetation type in Laikipia. It is often dominated by fever trees *Acacia xanthophloea* (Fabaceae). Other large trees in the riparian forest include Gerrard's acacia *Acacia gerrardii* (Fabaceae), *A. gracilior*, water pear *Syzygium guineense* (Myrtaceae)*,* water berry *Syzygium cordatum* (Myrtaceae), cape chestnut *Calodendrum capense* (Rutaceae), East African greenheart *Warburgia ugandensis* (Canellaceae), and figs *Ficus* spp. (Moraceae) (especially sycamore fig *F. sycomorus*).

The most widespread soil type on the plains of Laikipia is 'black cotton', which is *c.* 50% clay and *c.* 24% sand (Young *et al.* 1998). Bushland and woodland on black cotton is typically dominated by whistling thorn *Acacia drepanolobium* (Fabaceae) and/or euclea *E. divinorum.* Shrub and tree cover on black cotton in central Laikipia is *c.* 31% (Young *et al*. 1997; Riginos *et al*. 2009). Grass cover is more or less continuous. The more common grasses (Poaceae) include *Pennisetum stramineum*, *Pennisetum mezianum*, *Brachiaria lachnantha*, *Themeda triandra*, and *Setaria sphacelata*.

**Figure 1.** Location of Laikipia County (in red), Kenya.

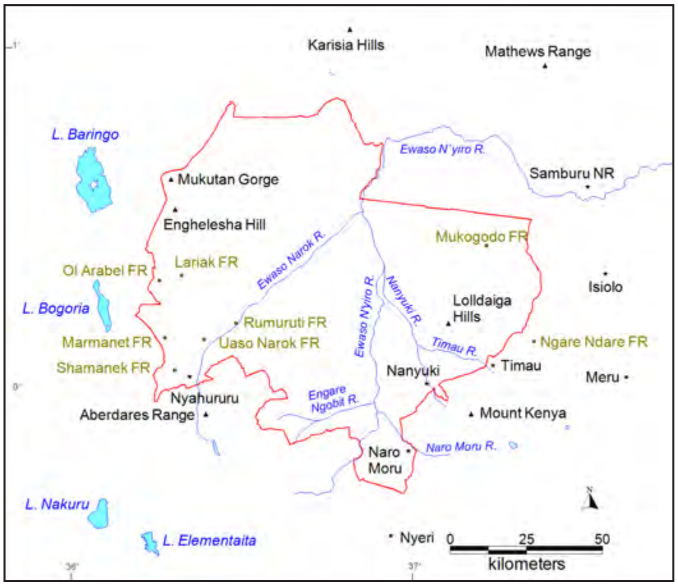

**Figure 2.** Laikipia County, central Kenya (outlined in red) with place names that are mentioned in the text. FR = Forest Reserve. NR = National Reserve.

The other widespread soil type in Laikipia is 'red sand', which is *c.* 74% sand and *c.* 15% clay (Augustine 2003a). Red sand typically supports bushland and woodland dominated by hook-thorn *Acacia mellifera*, savanna thorn *Acacia etbaica*, and wait-a-bit thorn *Acacia brevispica.* Other, often common, trees there are umbrella thorn *Acacia tortilis*, desert date *Balanites aegyptiaca* (Zygophyllaceae), small bead-bean *Maerua triphylla* (Capparaceae), and boscia *Boscia angustifolia* (Capparaceae). Shrub and tree cover on red sand in central Laikipia is *c*. 28% (Augustine 2003b). Grass cover there is usually discontinuous and, sometimes, sparse (Augustine *et al*. 2011). The more common grasses (Poaceae) include *Digitaria milanjiana*, *Cynodon dactylon*, *P. stramineum*, and *Chloris roxburghiana*. See LWF (2011) for more detailed information concerning the habitats and vegetation of Laikipia, and LWF (2011, 2013) for vegetation maps.

## Land Use in Laikipia

There are *c*. 400,000 people in Laikipia Country, approximately 76% of which live in rural areas (LWF 2013). Mean human population density is *c*. 42 people/km² (CAS 2013). Although some locations in south and south-west Laikipia have 100–300 people/km², most of Laikipia has <20 people/km². This population is expected to increase to 600,000 people by 2030 (LWF 2013).

Nearly 90% of Laikipia is too dry for cultivation (LWF 2013). About 65% (5,820 km²) is defined as wildlife habitat (Frank *et al*. 2005) and sizeable populations of most species of large wild mammals still occur there (Litoroh *et al*. 2010; Kinnaird *et al.* 2012; LWF 2012). At this time, *c.* 38% (3,650 km²) of Laikipia comprises relatively intact, contiguous, natural habitat managed in ways compatible with the maintenance of the original biodiversity, including the larger mammals. There is an area of similar size (*c*. 33%; 3,196 km²) of high potential wildlife habitat that is currently used in ways not compatible with the maintenance of the original biodiversity and over which large mammals are absent or nearly so (LWF 2012). In 2012, Kinnaird *et al.* (2012) found that 61% of the "observation cells" surveyed contained no large wild ungulates.

Black cotton soil and red sand soil are both suitable for livestock ranching (cattle, goats, sheep, camels), but poor for crop production. Laikipia's soils, semi-arid climate, and low availability of water, dictate that the only viable, sustainable, economic uses for most of the land are livestock production and tourism. Only 1.7% of Laikipia is classified as having high potential for agriculture, although, as of 1995, 8.4% was already under cultivation (Huber and Opondo 1995). As of 2013, 21% was occupied by small-holder farmers (LWF 2013). Attempts to grow crops in Laikipia on land that is not on the lower slopes of Mount Kenya or the Aberdares Range (where soil fertility and rainfall are highest) typically result in poor or no yields. A recent review of land use concluded that most of Laikipia's cultivation "is marginal, with detrimental effects on people and environmental health" (LWF 2013, p.5). Climate change is predicted to exacerbate this situation (LWF 2013).

Livestock ranching on privately-owned, government-owned, company-owned, or community-owned ("group ranches") rangeland is currently the primary economic activity in Laikipia. Over 80% of the people depend on livestock farming (CAS 2013). In 2011, large ranches and group ranches comprised 40% and 7%, respectively, of Laikipia. The ten largest ranches are each greater than 200 km², with the largest being 375 km². In 2011, 48% of Laikipia was tenured as rangeland and at least 29% was tenured as cropland (Table 1). Forest reserves and government land, together, comprise 14% of Laikipia. Both support livestock raising and crop production, but the size of the areas used for these activities is not known. Overall, in 2013, 37% of Laikipia was used for large-scale ranching, 32% was used by pastoralists, 21% was occupied by small-holder farmers (most of whom grow crops as well as graze livestock), and 5% was used exclusively for wildlife-based tourism (LWF 2013). Land-use maps for Laikipia are presented in Georgiadis (2011b), Kinnaird and O'Brien (2012), Kinnaird *et al.* (2012), and LWF (2012, 2013).

In Laikipia, rangeland management involves the removal of shrubs, trees, and invasive plants, burning of vegetation, manipulation of livestock numbers, movement of livestock, development and maintenance of sources of drinking water through dams and boreholes, and the control of large predators. The limiting resource for people, livestock and wildlife is most often water. The vast majority of the larger ranches encourage wildlife, tourism, and ecological/conservation research, and several have ecological/conservation training programs/centers. A number of ranches are managed primarily for the purpose of conserving Laikipia's biodiversity and some of these hold "Conservancy" status.

## Large Mammals and Primates of Laikipia

Unlike other semi-arid areas of this size in Kenya, including officially protected areas, Laikipia has not lost any

**Table 1.** Summary of land tenure types in Laikipia County, central Kenya, in 2011. Based on Letai (2011).

| Type of land tenure | Total area (km²) | Number of properties | Mean area (km²) | Percent of total land |
|---|---|---|---|---|
| Large scales ranches (rangeland) | 3,794 | 48 | 79 | 40.3 |
| Small holder farms (cropland) | 2,562 | 122 | 21 | 27.2 |
| Group ranches (rangeland) | 702 | 13 | 54 | 7.4 |
| Forest reserves | 701 | 12 | 58 | 7.5 |
| Government land (mostly rangeland) | 620 | 36 | 17 | 6.6 |
| Large scale farms (cropland) | 140 | 23 | 6 | 1.5 |
| Others | 880 | ? | ? | 9.4 |

species of indigenous large mammal. The large mammal fauna includes African buffalo *Syncerus caffer*, savanna elephant *Loxodonta africana*, giraffe *Giraffa camelopardalis*, black rhinoceros *Diceros bicornis*, wild dog *Lycaon pictus*, cheetah *Acinonyx jubatus*, leopard *Panthera pardus*, and lion *Panthera leo*. Laikipia is believed to hold the highest diversity of large mammal species of any site of its size in the world (T. M. Butynski and Y. A. de Jong pers. obs.).

With the exception of the Maasai Mara National Reserve, Laikipia supports higher densities of large wild mammals than any landscape in Kenya. In sharp contrast to major declines in large mammal numbers throughout Kenya, both inside and outside official protected areas, including the Maasai Mara (Western *et al.* 2009), Laikipia's populations of large mammals were, until recently, considered to be stable and, for some species, increasing (Georgiadis 2011b; Kinnaird and O'Brien 2012; LWF 2012). The most recent county-wide aerial census, however, indicates a decline between 2001 and 2012 in the abundance of 11 of 14 large ungulate species (Kinnaird *et al.* 2012).

Seven (37%) of Kenya's 19 species of non-human primate (De Jong and Butynski 2012) occur in Laikipia, of which two are galagos and five are monkeys. Of these seven species, three are forest-dependent and four are rangeland-dependent, two are nocturnal and five are diurnal, and four are arboreal and three are semi-terrestrial. The primate taxonomy applied in this article follows Butynski *et al.* (2013).

## Forest Primates of Laikipia

Over Laikipia, closed evergreen forest is limited to the vicinity of the larger rivers (riparian forest), the deeper valleys (gallery forest), and the higher ground. These forests cover but a small part of Laikipia (probably <6% or <600 km²). They are mostly associated with the larger rivers that flow off of Mount Kenya (for example, Naro Moru, Nanyuki, Timau) and Aberdares Range (for example, Upper Ewaso N'yiro, Engare Ongobit, Ewaso Narok), and with the higher ground where rainfall is greatest, mainly Mukogodo Forest Reserve and Ngare Ndare Forest Reserve in the north-east and, in the south-west, with the six forest reserves to the east of the Laikipia Escarpment/Eastern Rift Valley (i.e., Rumuruti, Uaso Narok, Shamanek, Marmanet, Ol Arabel, and Lariak Forest Reserves; Fig. 2).

Three of Laikipia's primate species are restricted to closed evergreen forest above *c*. 1800 m—Kolb's monkey *Cercopithecus mitis kolbi* (Fig. 3), Mount Kenya guereza *Colobus guereza kikuyuensis* (Fig. 4), and Kikuyu small-eared galago *Otolemur garnettii kikuyuensis* (Fig. 5). While all three are widely distributed over East Africa at the species level, at the subspecies level they are all endemic to the highlands of central Kenya (which include the Aberdares Range, Mount Kenya, Ngong Hills, and Nairobi; Fig. 1). These three species (and subspecies) are ranked as 'Least Concern' on the IUCN Red List (IUCN 2014).

The geographic range and abundance of these three subspecies of primate must have been greatly reduced over Laikipia during the past 100 years, largely through fragmentation of habitats and the conversion of closed evergreen forest to cropland (mainly wheat, maize and potatoes). Although these three subspecies are typically not compatible with Laikipia's cropland agroecosystem, they all, nonetheless, remain

**Figure 3.** Adult female Kolb's monkey *Cercopithecus mitis kolbi* in montane forest, Mount Kenya. Photograph by Y. A. de Jong and T. M. Butynski.

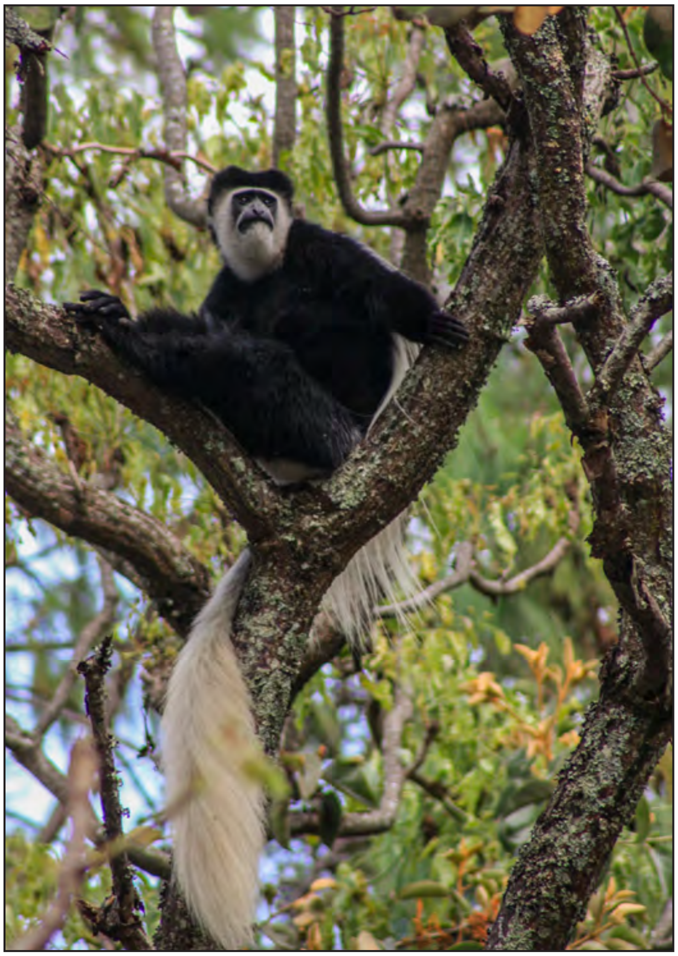

**Figure 4.** Adult male Mount Kenya guereza *Colobus guereza kikuyuensis* in montane forest, Naro Moru, Laikipia. Photograph by Y. A. de Jong and T. M. Butynski.

widespread and common elsewhere, particularly on the lower slopes (*c*. 1,800–2,900 m asl) of the nearby, contiguous, Aberdares Range and Mount Kenya (both of which are relatively well-protected). It is estimated that the geographic range of each of these three subspecies is >2,000 km², and that each numbers >10,000 individuals (Butynski 1999; T. M. Butynski and Y. A. de Jong pers. obs.).

Although the declining range and number of *C. m. kolbi, C. g. kikuyuensis*, and *O. g. kikuyuensis* in Laikipia is cause for concern and requires more investigation (see 'Recommendations'), the focus of this article is on the primates that occupy the other *c.* 94% of Laikipia—the primates of the rangeland agroecosystem.

## Rangeland Primates of Laikipia

Four species of non-human primate inhabit the semi-arid rangeland agroecosystem of Laikipia—eastern patas monkey *Erythrocebus patas pyrrhonotus* (Fig. 6), Hilgert's vervet monkey *Chlorocebus pygerythrus hilgerti* (Fig. 7), olive baboon *Papio anubis* (Fig. 8), and Kenya lesser galago *Galago senegalensis braccatus* (Fig. 9). All four species reach their highest density where the rangeland agroecosystem is well managed (i.e., used sustainably), and where hunting and trapping of primates (for example, in retaliation for crop damage) are not threats (as is the case in Laikipia's cropland agroecosystem). All four of these species (and their subspecies) are ranked as 'Least Concern' on the IUCN Red List (IUCN 2014).

*Erythrocebus patas* is by far the least abundant and widespread primate in Laikipia and, therefore, the primate of greatest conservation concern. This large (adult males weigh *c.* 12 kg), diurnal, omnivorous, semi-terrestrial, fast-running monkey occurs in low densities in East Africa (Isbell 2013) but can be locally common in northern Uganda (for example, in Kidepo National Park; T. M. Butynski and Y. A. de Jong pers. obs.). In Laikipia, the area over which groups of *E. patas* occur is roughly estimated at between 700 km² and 1,000 km² (T. M. Butynski and Y. A. de Jong pers. obs.). There, home ranges are 23–40 km² (Chism and Rowell 1988; Enstam and Isbell 2004), and densities are 0.2–1.5 individuals/km² (Chism and Rowell 1988; Isbell and Chism 2007).

**Figure 5.** Adult Kikuyu small-eared galago *Otolemur garnettii kikuyuensis* in riparian forest, Masinga Dam, central Kenya. Photograph by Y. A. de Jong and T. M. Butynski.

**Figure 6.** Adult male eastern patas monkey *Erythrocebus patas pyrrhonotus* in whistling thorn acacia *Acacia drepanolobium* woodland, Ol Pejeta Conservancy, Laikipia. Photograph by R. Copeland.

**Figure 7.** Hilgert's vervet monkey *Chlorocebus pygerythrus hilgerti* adult females with young in mixed acacia woodland, Borana Conservancy, Laikipia. Photograph by Y. A. de Jong and T. M. Butynski.

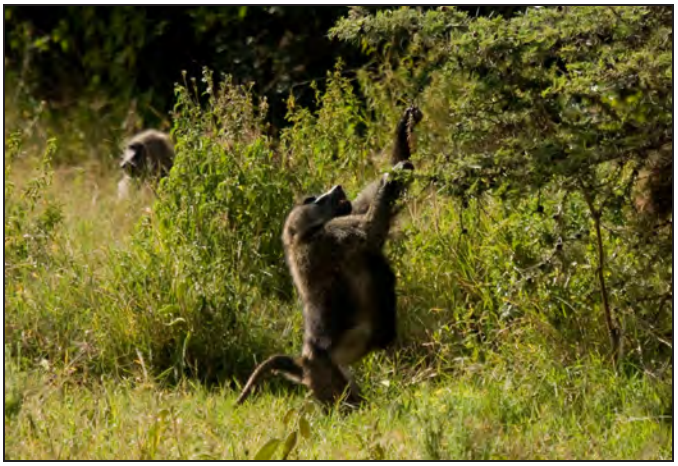

**Figure 8.** Adult male olive baboon *Papio anubis* feeding from whistling thorn acacia *Acacia drepanolobium*, Lolldaiga Hills Ranch, Laikipia. Photograph by Y. A. de Jong and T. M. Butynski.

**Figure 9.** Adult Kenya lesser galago *Galago senegalensis braccatus* in mixed acacia woodland, Ol Pejeta Conservancy, Laikipia. Photograph by Y. A. de Jong and T. M. Butynski.

In Laikipia, the preferred habitat is open savanna woodland dominated by *Acacia* spp., particularly *A. drepanolobium* (Chism and Rowell 1988; Enstam and Isbell 2002; Isbell 2013). There, *A. drepanolobium* comprises >80% of the diet in the form of gum, flowers, seed pods, and arthropods (Isbell and Chism 2007; Isbell and Young 2007; Isbell 2013).

*Erythrocebus patas* populations are declining in East Africa while geographic ranges are shrinking and fragmenting. From 1996 to 2008, the geographic range of *E. patas* in Kenya declined by *c*. 46% (De Jong *et al*. 2008), and from 1995 to 2009, the geographic range in Tanzania declined by *c*. 33% (De Jong *et al*. 2009). Although Laikipia is thought to support the largest population of *E. patas* in Kenya (Isbell and Chism 2007; De Jong *et al*. 2008), the population is, nonetheless, small. This population appears to have been stable between 1979 and 2000 (415 individuals in 14–15 groups in 1979; 310–445 individuals in 13–17 groups in 2000 [Isbell and Chism 2007]). Preliminary findings from a current survey indicate, however, that this population has declined since 2000 (Y. A. de Jong and T. M. Butynski pers. obs.).

*Chlorocebus pygerythrus* is a medium-sized (adult males weigh *c.* 4 kg), diurnal, omnivorous, semi-terrestrial monkey, that is patchily distributed and locally common in Laikipia and over much of Kenya. It has home ranges of 10–40 ha in Laikipia (Isbell *et al*. 2002), and occurs at densities of 9–80 individuals/km² (Isbell and Enstam 2002; Isbell 2013). *Chlorocebus pygerythrus* is strongly associated with perennial and seasonal watercourses where there is *A. xanthophloea* woodland adjacent to *A. drepanolobium* bushland/woodland (Isbell *et al.* 2002). In one study in Laikipia, *A. drepanolobium* and *A. xanthophloea* accounted for *c.* 35% and 22% of the diet, respectively (Pruetz and Isbell 2000).

*Papio anubis* is a large (adult males weigh *c.* 22 kg), diurnal, omnivorous, semi-terrestrial monkey that is common in grassland, bushland, and woodland over much of Laikipia (Palombit 2013). There, home range size varies from <15 km² (T. M. Butynski and Y. A. de Jong pers. obs.) to >44 km² (Barton *et al*. 1992). Diet is composed of a very large number of food items, including leaves, flowers, seeds, fruits, gum, and underground parts, taken from grasses, herbs, and trees (Barton *et al.* 1992).

*Galago senegalensis* is a small (adult males weigh *c.* 225 g), nocturnal, omnivorous, mostly arboreal, prosimian that is widespread through the bushland and woodland of Laikipia. Limited data for this species in Laikipia indicate that the home range is roughly 4 ha and that densities are typically 40–240 individuals/km² but can be much lower and much higher than this (Nash and Whitten 1989; Off *et el.* 2008; Nash *et al*. 2013; T. M. Butynski and Y. A. de Jong pers. obs.). This species is widespread in *A. drepanolobium* bushland/woodland but reaches its highest densities in *A. xanthophloea* woodland. The diet includes mainly invertebrates and acacia gums, particularly of *A. drepanolobium* and *A. xanthophloea* (Nash and Whitten 1989; Nash *et al.* 2013).

The distribution and abundance of the four primate species in the Laikipia rangeland agroecosystem can be explained, not surprisingly, by the availability of water, food, and secure sites for sleeping and refuge. *Papio anubis*, *C. pygerythrus*, and *E. patas* require perennial sources of drinking water and will drink daily where water is readily available (Chism and Rowell 1988; Isbell and Chism 2007; De Jong *et al*. 2008). These three species probably do not occur anywhere in Laikipia where they cannot drink at least once every two days. At sites far from natural perennial sources of water, these three monkeys would not occur except for the constant presence of water at tanks and troughs placed for livestock. *Galago senegalensis* does not need to drink and, thus, its occurrence is not affected by the availability of water.

All four species require secure sites in which to rest, sleep, and take refuge from predators; in Laikipia, *P. anubis* uses tall trees and large, steep rock faces, *C. pygerythrus* uses tall trees, *E. patas* uses small to medium-sized trees (0.5–6.0 m tall) in open woodland, and *G. senegalensis* uses tree holes or trees with dense foliage in which nests are constructed (Chism and Rowell 1988; Enstam and Isbell 2002; Off *et al*. 2008; Isbell 2013; Isbell and Enstam Jaffe 2013; Nash *et al.* 2013; Palombit 2013; T. M. Butynski and Y. A. de Jong pers. obs.).

The removal by humans of natural resources from the rangelands may represent competition with one species of primate while enhancing the carrying capacity of the site for another. For example, it is likely that the partial removal of *A. drepanolobium* from a site (for firewood and the production of charcoal) reduces the carrying capacity for *G. senegalensis* and *E. patas* while increasing the carrying capacity for *P. anubis* and *C. pygerythrus*.

## Benefits to Laikipia's Primates of Livestock Ranching

As mentioned briefly above, ranching in the rangeland agroecosystem of Laikipia can benefit all four species of primate or is, at worse, a neutral land use activity as concerns primate conservation. Here are some examples of known and suspected benefits:

1. Most, if not all, large ranches have established, and maintain, water tanks and water troughs throughout the property. These perennial sources of water enable *E. patas*, *C. pygerythrus* and *P. anubis* to access these areas to forage and make use of the secure sleeping and refuge sites nearby (Chism and Rowell 1988; De Jong 2004; Isbell and Chism 2007; De Jong *et al.* 2008).
2. Most, if not all, large ranches have established, and maintain, systems of dams that serve as perennial sources of water, or, at least, maintain water for extended periods. These sites not only provide drinking water for primates and other wildlife, they also promote and support large trees (particularly *A. xanthophloea* and *Ficus* spp.) that provide important foraging, sleeping and refuge sites for all four primate species in the rangeland (Y. A. de Jong and T. M. Butynski pers. obs.).
3. *Erythrocebus patas*, *C. pygerythrus*, and *P. anubis* often seek high perches on which to rest and scan the surroundings. Fence posts are frequently used perches in open areas. In addition, *E. patas* often moves along the woodland edges that the fence lines typically create (Chism and Rowell 1988).
4. Privately-owned, government-owned, and company-owned ranches protect extensive areas of *A. drepanolobium* bushland/woodland and *A. xanthophloea* woodland. Also, the community-owned group ranches are coming to appreciate the value of these habitats, taking measures to conserve them at some sites. These are critical habitats for the primates of Laikipia.
5. Prickly pears *Opuntia* spp. (Cactaceae), introduced to Laikipia from South America in the 1950s for use as 'living fences' (Vernon 2008), are common at some sites. *Opuntia* spp. are an important source of food and water for all three monkeys, particularly during times of severe drought (Chism and Rowell 1988; Strum *et al*. in press; D. Manzolillo-Nightingale pers. comm.; Y. A. de Jong and T. M. Butynski pers. obs.). *Galago senegalensis* is also suspected of making use of *Opuntia*.
6. Predation on semi-terrestrial primates can be severe (Isbell *et al*. 2009). Predators of primates (for example, leopard, lion), although common in some parts of Laikipia, continue to be persecuted in the name of livestock protection, particularly on the group ranches (Frank *et al.* 2005; Woodroffe and Frank 2005; Frank 2011). Reduced predator densities may allow for higher primate densities, as well as enable the semi-terrestrial *E. patas*, *C. pygerythrus*, and *P. anubis* to forage more efficiently over larger areas (i.e., farther from secure retreats such as large trees and cliffs).
7. Transmission of diseases and parasites between humans and non-human primates, and the related morbidity and mortality, is of considerable concern (Butynski 2001; Chapman *et al.* 2006; Estrada *et al.* 2012; Young *et al.* 2013). Given the much lower human and domestic animal population densities in Laikipia's rangeland agroecosystem compared to the cropland agroecosystem, and the greater aridity of the rangelands, the incidence of disease and parasite transmission between humans and non-human primates is likely to be significantly less in the rangeland agroecosystem. There is, however, insufficient research on this topic for Laikipia. This is a priority area of research as concerns Laikipia's primates.
8. A large number of stakeholders concerned with the well-being of Laikipia's environment, particularly its wildlife, water and natural habitats, are promoting conservation actions. Conservation and ecotourism associations and partnerships have been created, and ecological/conservation research centers established, to work towards maintaining sustainable populations of wildlife and livestock for the long-term benefit of the people of Laikipia (Kinnaird and O'Brien 2012; Galvin and Reid 2014). At the center of these actions is the Laikipia Wildlife Forum (LWF 2011, 2013). This forum includes the owners of large ranches, group ranches, and other properties. In 2012, LWF produced a strategic conservation plan, *The Wildlife Conservation Strategy for Laikipia County (2012–2013)* (Didier *et al.* 2011; LWF 2012). The goal, as stated in this plan is "By 2030 the people of Laikipia perceive wildlife as a valuable asset and the diversity and populations of native species have been maintained or increased." Of the 21 'targets' put forth in this plan, the following six, if achieved, are likely to have the greatest positive impact on the long-term conservation of Laikipia's seven species of non-human primate:
    - By 2030 the owners of the 3,650 km² of existing habitat that currently supports most of Laikipia's wildlife are committed to wildlife conservation as a form of land use.
    - By 2030 owners of at least half of the 3,196 km² of existing high potential wildlife habitat (where wildlife is currently absent or found in low numbers) are committed to wildlife conservation as a form of land use.
    - By 2030, within the context of stable wildlife populations, more than half of Laikipia's residents view wildlife as an asset.
    - By 2030 the area under upland forest has increased by 50%.
    - By 2030 the Ewaso N'yiro River and its tributaries flow year round.
    - By 2030 wildlife is able to move unhindered within Laikipia and between Laikipia and the adjacent ecosystems.

### Conflict between Humans and Non-human Rangeland Primates

The rangelands occupied by *E. patas*, *C. pygerythrus*, *P. anubis*, and *G. senegalensis* in Laikipia vary from relatively pristine and extensive (>1,000 km²) to extremely degraded and fragmented (<1 km²). Little or no competition exists between the four primates and livestock for food and water, and, in the absence of crops, competition between the four primates and humans is low, particularly when compared to the level of conflict in the cropland agroecosystem (see above and below). That said, here are a few examples of livestock-primate and human-primate conflicts that are known to occur, or probably occur, in the Laikipia rangeland agroecosystem:

1. Habituated *C. pygerythrus* and *P. anubis* sometimes raid tourist lodges, houses, and camp/picnic sites for food (Y. A. de Jong and T. M. Butynski pers. obs.).
2. Adult *P. anubis* predation on young sheep and goats, and chickens and chicken eggs, is widespread and common, particularly on the group ranches. There is, however, considerable variation in frequency with time and place; predation on livestock seems to be most frequent during the dry season when natural foods are most scarce (Strum 2010; C. Muhoro and T. M. Butynski pers. obs.).
3. *Chlorocebus pygerythrus* and *G. senegalensis* occasionally raid beehives and extract honey, and *G. senegalensis* sometimes nests in beehives (M. Kelly pers. comm.; T. M. Butynski and Y. A. de Jong pers. obs.).
4. There are probably occasions, in times of food scarcity (for example, during droughts), when *C. pygerythrus* and *P. anubis* compete with goats for wild fruits.
5. *Papio anubis* (particularly) and *C. pygerythrus* are among the more important dispersers of the seeds of prickly pear, especially *Opuntia stricta*. These are common to abundant invasive plants on Laikipia's more degraded rangelands. As noted above, however, *Opuntia* spp. are not "all bad" as they provide important dry-season/drought foods for some species of livestock and wildlife (Vernon 2009; Strum *et al.* in press), including *P. anubis* and *C. pygerythrus*.

Primates are, overall, rather easy for pastoralists and ranchers to coexist with. There is little primate-human conflict in the rangeland agroecosystem, in strong contrast to the situation in Laikipia's cropland agroecosystem, where primate-human conflict is typically high and no species of monkey is tolerated. The hunting of primates for bushmeat is not considered a threat for any of Laikipia's primates as the people of Laikipia seldom, if ever, eat them.

## Threats to Primates in Laikipia

In some parts of Laikipia the rangeland has been severely degraded and fragmented due to over-grazing and over-browsing by livestock, and by the unsustainable cutting of trees for firewood and charcoal. This over-exploitation threatens Laikipia's four species of rangeland-dependent primates.

To provide land to the growing human population of Laikipia, the Government of Kenya has sometimes purchased large ranches on which there is prime wildlife habitat and thriving wildlife populations and then subdivided these into 1–10 ha plots (Mucuthi and Munei 1996; Letai 2011). Once settled by farmers, the conservation values of these small plots rapidly decline as the conversion from a rangeland agroecosystem to a cropland agroecosystem takes place. Conversion of prime rangeland to cropland not only greatly reduces the natural foods and secure sites for all four of Laikipia's rangeland primates, it puts the three species of monkey into direct competition with humans for food (Isbell and Chism 2007; De Jong *et al*. 2008; Strum *et al*. 2008; Isbell 2013). In other words, all three species of monkey become serious crop pests for which Laikipia's farmers have no tolerance.

The water of the few perennial rivers of Laikipia (none of which is large) is increasingly exploited for the irrigation of crops. This removal of water is currently heavy and poorly managed, and greatly affects river flow. This problem is exacerbated by the considerable damage to natural vegetation in the water catchments on Mount Kenya, the Aberdares Range, and Laikipia Plateau. During the drought of 2009, the major river of Laikipia, the Ewaso N'yiro, stopped flowing for the first time in living memory; for several months the only water in this river was in widely scattered pools. The land along the perennial rivers of Laikipia comprises part of the home ranges of numerous groups of *C. pygerythrus* and *P. anubis*. Where these rivers are the only source of perennial water in the area, *C. pygerythrus* forages a few hundred meters from the river and *P. anubis* forages a few kilometers from the river. If long stretches of these rivers were to hold no water for extended periods, these two species would no longer be able to use the areas on a year-round basis. This would result in a serious decline in the abundance of both species in Laikipia.

Habitat fragmentation is one of the main threats to the conservation of species, including primates (Schwitzer *et al*. 2011; Estrada *et al*. 2012). Kenya's protected area system, as elsewhere in Africa, is not, alone, adequate to support the long-term survival of many of the large species of mammal (Craigie *et al*. 2010). As such, maintaining connectivity among Kenya's major protected areas through the conservation of lands that are not officially protected is crucial to the maintenance of the nation's large mammal biodiversity.

At present, Laikipia's rangeland agroecosystem, where well managed, provides considerable habitat connectivity among several of Kenya's largest and most important ecosystems for the conservation of biodiversity, particularly for primates and large mammals (Didier *et al*. 2011; Georgiadis 2011b). These sites include the Mathews Range and Samburu Ecosystem to the north, Meru Ecosystem to the east, Mount Kenya to east and south-east, the Aberdares Range to the south-west, and the Eastern Rift Valley to the west (Fig. 2). The current expansion of the cropland agroecosystem, together with new settlements and poorly managed rangelands on some group ranches, are reducing this connectivity. One of the several negative consequences of this loss of connectivity is that options for the movement of primates, large wild mammals, and other species, are reduced, thereby threatening the viability of their populations.

## Conclusions

The wildlife in the rangeland agroecosystem of Laikipia has ecological, scientific, financial and aesthetic value (for example, Shorrocks 2007, LWF 2013), and ethical arguments can be put forth for its conservation. Large parts of Laikipia's rangeland are, however, undergoing extensive and rapid transformation due to increasing livestock and human densities, and the demand that this puts on natural resources (Vernon 2008; LWF 2012). The resulting loss of natural habitat, soil, and productivity, damage to the watershed, together with expanding villages and towns, are not only threatening human livelihoods and cultures, but Laikipia's biodiversity, including its four species of non-human rangeland primates. This degradation and loss of Laikipia's natural habitats through unmanaged human use poses an enormous challenge to the integrity of this landscape (LWF 2012).

Three of the primates remain common in this rangeland agroecosystem, while one, *E. patas*, is under threat of extirpation (not only from Laikipia but also from Kenya and Tanzania). Conversion of the rangeland agroecosystem to a cropland agroecosystem is a threat to the survival of all four species as none can thrive in a cropland agroecosystem where there are high human densities and/or intensive agriculture; *E. patas* is the least tolerant, followed by *P. anubis, C. pygerythrus*, and *G. senegalensis*. The larger primates with large home ranges are less able to survive in the cropland agroecosystem than are the smaller primates with small home ranges.

## Recommendations

Concerning the long-term conservation of the seven species of non-human primate in Laikipia, our present understanding of their status, threats, and ecology/behavior leads to the following four recommendations:

1. ***Erythrocebus patas* should be the focus for primate conservation research and action in Laikipia.** In Laikipia, the most specialized primate, the one in lowest numbers, and the one under greatest threat, is *E. patas*. This small, isolated, population is judged to be vulnerable to extirpation, especially via stochastic events, particularly disease and social/political unrest. Correctly focused efforts on behalf of *E. patas* in this rangeland agroecosystem appear to be essential to increasing the size and geographic range of this population. A better understanding is needed of what limits the distribution and abundance of *E. patas* in Laikipia with the aim of determining how ranch management and other practices can be altered to promote the growth of this population (also De Jong and Butynski 2011). If conditions in Laikipia are such that *E. patas* can survive, all other species of primate on Laikipia's rangelands will also survive.
2. **Habitat conservation in Laikipia should be on water-associated vegetation types and the adjacent *A. drepanolobium* woodland, particularly along the Ewaso N'yiro River and its major tributaries.** Conservation of, and access to, the perennial water sources (springs, rivers, ponds, swamps) of Laikipia, and their associated natural vegetation types (water-edge forest and large-tree woodland), is critical to the survival of all five of Laikipia's species of monkey, as well as to humans. In addition, for *E. patas* to survive in Laikipia, large areas of *A. drepanolobium* woodland adjacent to these more mesic vegetation types need to be conserved. Conservation of the long, linear, water-associated habitats of Laikipia, and of adjacent *A. drepanolobium* woodland, would enable gene flow for all five species of monkey, as well as for the long-term conservation of most of Laikipia's other species, both animal and plant.
3. **Develop primate-based tourism in Laikipia.** With few exceptions, little attention has been given to promoting primate-based tourism in Laikipia. This activity can, however, with little effort or expense, generate additional revenue, employment, and interest in primate conservation. At present, with the exception of *E. patas* and *O. garnettii*, all species of primate in Laikipia (both diurnal and nocturnal) can been readily located and observed at multiple sites, either on foot or from a vehicle. Ample numbers of semi-habituated, readily observed primates, which could serve as the focus of this tourism activity, are already present in Laikipia. Feeding primates for the purpose of habituation should not be allowed, nor should the creation of super-habituated primates. Such primates invariably become a problem and are either removed or, more often, destroyed.
4. **Conduct primate surveys in Laikipia's eight Forest Reserves.** As mentioned above, there are eight Forest Reserves in Laikipia. These harbor most of the county's closed evergreen forest and its three species of forest-dependent primates, all of which are represented by subspecies endemic to the highlands of central Kenya (*C. m. kolbi*, *C. g. kikuyuensis*, and *O. g. kikuyuensis*). No primate surveys have been conducted in any of these forest reserves. Surveys should be undertaken to assess primate species diversity, distribution, abundance, threats and conservation status, as well as the integrity of, and threats to, these forests.

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# The First Survey of the Conservation Status of Primates in Southern Burkina Faso, West Africa

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**Abstract:** Little is known about the extent of primate abundance and distribution in Burkina Faso, West Africa. Only two prior surveys have been reported, each in just one protected area and one dating as far back as 1976. With this study, we aimed to update our understanding of primate presence in Burkina Faso. Between 11 May and 16 July 2012, we surveyed nearly 250 km in five protected areas along the southern border of the country, collecting data on the presence of primates, predators, and poaching activities. Although several sources have listed up to nine primate species as present in Burkina Faso, we were only able to confirm five of four genera: *Galago senegalensis*, *Papio anubis*, *Erythrocebus patas*, *Chlorocebus sabaeus*, and *Chlorocebus tantalus*. With the results of the surveys, and in-depth interviews with 24 workers, farmers and protected area officials, we indicate that *Pan troglodytes verus* has been extirpated from Burkina Faso, and that *Colobus vellerosus* and *Cercocebus lunulatus* are either already gone or are close to extirpation. We report encounter rates for *Papio anubis*, *Erythrocebus patas*, *Chlorocebus*, *Panthera leo*, *Panthera pardus*, and poaching activities. The threats to the remaining primate species include legal and illegal hunting, and inconsistent and ineffective law enforcement in protected areas. Agricultural expansion will continue to rise as a threat to these species, particularly *Papio anubis* and *Erythrocebus patas*, through habitat alteration as well as increasing human-wildlife conflict over crop-feeding behaviors.

**Key Words:** *Colobus vellerosus*, *Cercocebus lunulatus*, *Chlorocebus*, *Galago senegalensis*, *Erythrocebus patas*, *Papio anubis*, reconnaissance

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## Introduction

The landlocked country of Burkina Faso, West Africa, encompasses a range of ecosystems, from the Sahelian deserts bordering Mali in the north to the savanna woodland mosaics along the borders of Côte d'Ivoire and Ghana in the south. The southern portion of Burkina Faso marks the outer limits for the ranges of several West African primates, though little research has been conducted to determine their presence, distribution and abundance in the country. Although nine primate species have been reported as occurring in Burkina Faso (see Table 1), including *Pan troglodytes verus*, only two primatological surveys had been conducted. Nearly 40 years ago, Poché (1976) reported the presence of *Galago senegalensis*, *Erythrocebus patas*, *Papio anubis*, and *Cercopithecus aethiops tantalus* (now *Chlorocebus tantalus*) in W National Park, southeastern Burkina Faso.

Galat and Galat-Luong (2006), following a six-day survey in the southwestern Comoé-Léraba Partial Reserve, reported sightings of *E. patas*, *Chlorocebus sabaeus*, *Colobus vellerosus*, and *Cercocebus atys lunulatus*. Populations of *Colobus vellerosus* have declined by more than 30% over the last 30 years, and the species has been classified as Vulnerable since 1994. Gonedelé-Bi *et al*. (2010) argued that it should be ranked as Endangered. Populations are often too small for estimates; they are present in neighboring Ghana, Togo, Benin and Côte d'Ivoire but may be extinct in Nigeria (Oates 2011).

The white-naped mangabey *Cercocebus atys lunulatus* is now considered a full species, *C. lunulatus* (see Oates 2011). *Cercocebus lunulatus* was listed as one of the World's 25 Most Endangered Primates in 2005 (McGraw *et al*. 2005). Its range is now limited to only a few forest patches in Ghana (Oates 2000, 2011) and Côte d'Ivoire (Fischer *et al*. 2002; Gonedelé Bi *et al*. 2008), with all wild populations threatened by illegal hunting (Oates 2011). Populations are thought to have decreased by at least 50% over the last few decades (Oates *et al.* 2008b).

Grubb *et al.* (1998) followed Booth (1956) in indicating that *Chlorocebus sabaeus* occurs to the west of the White Volta River in Ghana, and is replaced by *C. tantalus* to the east of the river and on the Accra Plain. Haus *et al.* (2013) have recently reported on the geographic distribution of *C. sabaeus* and *C. tantalus* in Burkina Faso however, and the easternmost sample of *C. sabaeus* was from Krachi, east of the White Volta River in Ghana. They suggested that the Oti or Pendjari River, a left bank tributary of the Volta River, not the White Volta as Booth suggested, separates the two species in Ghana and Burkina Faso. The westernmost limits for *C. tantalus* are still not clearly defined, however, and hybridization within the contact zone of *C. tantalus* and *C. sabaeus* is likely (Haus *et al.* 2013).

The only direct report of a galago in Burkina Faso comes from Poché (1976), but both *Galago senegalensis* and *Galagoides demidovii* have been listed as present (Table 1). While the wide distribution of *G. senegalensis* across the continent makes its presence likely, there are currently no direct accounts of *G. demidovii*—either live or through trade—in Burkina Faso. The case for *P. t. verus* is similar. Scant reports of at least seasonal migrations from Côte d'Ivoire were reported by Teleki (1989), with occasional sightings reported across the southern border of the country (Redmond, pers. comm.; Redmond 2005). No surveys had been conducted, however, and at the time of this study, no new reports had been documented for decades.

Of the nine species considered present in Burkina Faso, the IUCN Red List (IUCN 2014) classifies two as Endangered (*P. t. verus* and *Cercocebus lunulatus*) and one as Vulnerable (*Colobus vellerosus*) (Table 1). *Erythrocebus patas* is classified as Least Concern but is in decline (Kingdon *et al.* 2008). *Papio anubis*, also Least Concern, is recorded as increasing in numbers. The remaining four (*Galagoides demidovii*, *Galago senegalensis*, *Chlorocebus sabaeus* and *C. tantalus*) are considered Least Concern with stable or increasing populations.

The human population of Burkina Faso is extremely poor. The country is ranked as the fifth least developed by the United Nations' Human Development Report (UNDP 2013), and it is the eighth fastest growing population (CIA 2013). This rapid population growth is contributing to the overexploitation of land and, with 90% of the population relying on subsistence agriculture, we can expect agricultural land conversion and land degradation to continue and worsen (Bance *et al*. 1999; Kristensen and Lykke 2003; CIA 2013). As of 1999, only 14% of Burkina Faso's land cover and 25% of forests were within protected areas (Bance *et al*. 1999). Law enforcement is weak (Gnoumou *et al*. 2011), allowing the threats of agricultural expansion and illegal hunting of wildlife to persist even in national parks and reserves. In protected areas around the world, hunting is a greater threat to wildlife than habitat loss (Fa *et al*. 2005; Kümpel *et al*. 2008), particularly for large mammals, including primates.

Primate population estimates and distribution data are needed in order to monitor and mitigate the effects of habitat loss, degradation and fragmentation, and hunting on the primates of Burkina Faso. Our aim here is to provide a preliminary assessment of the primates of Burkina Faso to be used as baseline information for future comparative analyses, and to narrow future research inquiries. Our objectives were to (a) investigate the presence/absence and relative distribution of Burkina Faso's primates, (b) gather follow-up data on the status of *Cercocebus lunulatus*, *Colobus vellerosus*, and *Pan troglodytes verus* in Comoé-Léraba Partial Reserve, and (c) determine the potential or actual threats to primate habitats in southern Burkina Faso. The unfortunate results regarding the likely extirpation of *Pan troglodytes verus* from this historic range country were reported by Ginn *et al*. (2013), and here we focus on the other eight primates.

## Methods

### *Survey areas*

We (Ginn, research assistants, and locally hired guides and translators) surveyed along 237.73 km in five protected areas across the southern border of Burkina Faso as follows: Pama Partial Reserve, Kompienga province (36.45 km); Arly National Forest, Gourma province (50.37 km); Comoé-Léraba Partial Reserve, Comoé and Léraba provinces (55.21 km); Koulbi Protected Forest, Poni province (47.40 km); and Nazinga Game Ranch and Reserve, Nahouri province (48.30 km) (Figs. 1 and 2). These sites are in the South Sudanian sector of Burkina Faso, characterized by 900–1100 mm of annual rainfall and rich soils (Sambaré *et al*. 2011), and a shrub-forest mosaic (Fig. 1). The protected areas are government-owned lands, and managed by the Burkina Faso Ministry of Environment (MOE) except for Comoé-Léraba which is managed by the *Association interVillageoise de Gestion des Resources Naturelles et de la Faune* (AGEREF/CL).

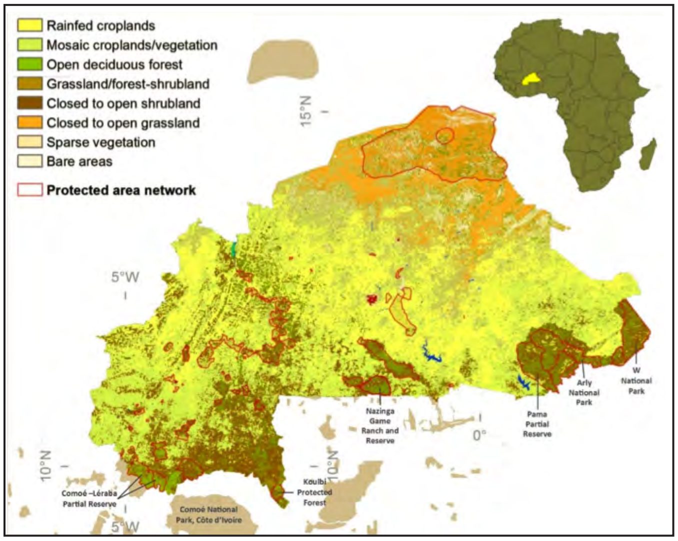

**Figure 1.** Vegetation zones and protected areas of Burkina Faso, West Africa.

AGEREF/CL is a cooperative of eleven bordering communities that share fishing rights and access to forest resources for the sale of shea butter, honey, and fuelwood. Seasonal hunting, mostly by international hunters, of primarily ungulates but also the occasional primate, provides the cooperative with an additional source of income. Comoé-Léraba is in the most biodiverse region of Burkina Faso, particularly in its riparian forests (Sambaré *et al*. 2011). This region is facing several threats, namely agricultural expansion in and around the reserve, desertification, and an increase in illegal hunting activities. Poaching activities in bordering northern Côte d'Ivoire increased dramatically during and after the country's political unrest of the early 2000s (Fischer 2004); with decreasing wildlife already noted in Comoé-Léraba (Bance *et al*. 1999), we expected the Ivorian political unrest and increase in poaching to have negatively impacted Comoé as well.

Pama Partial Reserve and Arly National Park, in the southeast of Burkina Faso, are part of what is often referred to as the WAP Complex: W National Park (a transfrontier collaborative of Benin, Burkina Faso and Niger), Arly National Park (including bordering Pama Partial Reserve) and Pendjari National Park, Benin (Clerici *et al*. 2007). This network of protected areas is best known for hosting the largest population of *Loxodonta africana* in West Africa (Bouché *et al*. 2011). Seasonal hunting is permitted in Pama, with the assistance of guides hired through either the local MOE office or from nearby safari lodges. Neighboring Arly National Park, however, is strictly protected. In its peak, roughly 10,000 tourists visited Arly per year, using a local airport for access. The airport and the on-site tourist lodge have both closed, and access roads have deteriorated, nearly eliminating the flow of tourism and thus income to the park.

Nazinga Game Ranch and Reserve, in south-central Burkina Faso, is the most consistently managed and well-studied of Burkina Faso's protected areas and, likely as a result, has experienced large mammal population increases. Bouché *et al*. (2011) estimated that populations of *Loxodonta africana* more than doubled between 1991 and 2010, and Marchal *et al*. (2010) found that between 2001 and 2010, most ungulate populations in the western portion of Nazinga increased. The reserve conducts regular anti-poaching patrols, engages in community outreach with 12 neighboring villages, and is easily accessed from the capital, Ouagadougou, by both wildlife tourists and international hunters.

The newest protected area in Burkina Faso, Koulbi Protected Forest was created in 2009 through the displacement of 14 villages. The park is bordered on the west by Côte d'Ivoire and on the east by Ghana, creating more international access than the other study sites. At the time of this study, several families were secretly living, hunting and farming in the forest, and there was limited presence or enforcement of the law.

### *Survey methods*

We collected data between 11 May and 16 July 2012 through reconnaissance (recce) surveys. Recces follow paths of least resistance, covering only new ground; they provide the ability to survey four times more land than line transects (Walsh and White 1999). During the recces, we walked at

**Figure 2.** The typical habitat types of the five protected areas surveyed: (A) Pama Partial Reserve, (B) Arly National Park, (C) Nazinga Game Ranch and Reserve, (D) Comoé-Léraba Partial Reserve, and (E) Koulbi Protected Forest. Photos A and B by Josh Robison. Photos C, D, and E by Laura Ginn.

speeds of 1–3 km/hr (average 1.25 km/hr), documenting with Garmin 60CS GPS all signs of primate presence (sightings as well as secondary signs such as feces, tracks, vocalizations, evidence of feeding), predator signs and signs of presence, and all instances of anthropogenic disturbances and poaching activities (shotgun shells, human tracks, poaching camps, gunshots heard, and traps or snares). Because data were collected outside of the legal hunting season, we were able to consider all signs of hunting as poaching activities. Encounter rates were too low to use the DISTANCE software, so we analyzed the data using descriptive statistics and compared the results to poaching and predator encounter rates using non-parametric Spearman's Rho (Dytham 2011). In addition, we conducted nocturnal surveys in each location except Nazinga, for a total of at least 11.58 km (some nocturnal GPS data were corrupted). We employed the same methods as the diurnal recces, using red-filtered headlamps to search for the reflective gaze of galagos (Perkin 2006). Sightings were photographed for later identification by Nekaris and the Nocturnal Primate Research Group based at Oxford Brookes University.

To supplement the survey findings, we conducted semi-structured interviews with park management, guides, and farmers regarding management, anti-poaching policies, and human-wildlife conflicts. Interviewees (N = 24) had an average of 23 years of working knowledge in their respective locations. The interviews were conducted in the interviewees' preferred language using a locally hired, English-speaking translator. Participants were shown photographs of 22 animals, nine of which known to not occur in Burkina Faso. The remaining 13 pictures were the presumed nine species of primates, *Loxodonta africana*, *Lycaon pictus*, *Crocuta crocuta* and *Hippopotamus amphibius*. This method was used to test for individual reliability based on the methods of De Jong *et al*. (2008). Participants were asked to identify which animals they have seen in their respective forests, after which we asked follow-up questions regarding perceived distribution, abundance, and human-primate interactions

This research was approved by the Oxford Brookes University Research Ethics Committee, the *Centre National de la Recherche Scientifique et Technologique du Burkina Faso*, and the Burkina Faso Ministry of Environment. Interviews were also approved by local MOE authorities and village chiefs.

## Results

Of the nine species believed to be present in Burkina Faso, we confirmed five in four genera: *Galago senegalensis*, *Papio anubis*, *Erythrocebus patas*, *Chlorocebus sabaeus*, and *Chlorocebus tantalus* (Table 1).

### *Galago senegalensis*

No galagos were observed in the study sites, though we did encounter two individual *Galago senegalensis* on the southwestern range of Pama, near Yaryanga Safari and the village of Pama (Table 1; Fig. 3). Interviewees quickly recognized photographs of *G. senegalensis* and reported that the animals prefer fruiting shea butter (*Vitellaria paradoxa*: Sapotaceae) trees in or near villages and cities, including the capital of Ouagadougou.

### *Papio anubis*

We encountered a total of 17 troops of baboons in four of the study sites, with an average observed group size of 7.12 individuals. *Papio anubis* was not seen in Koulbi. Group encounter rates were highest in Nazinga (0.166/km) and Arly (0.099/km) (Fig. 4). Pama and Comoé had lower, and comparable, encounter rates of 0.042/km and 0.037/km, respectively (Tables 2 and 4). Like *E. patas* (see below), *P. anubis* was reported to feed frequently on crops, and baboons were also reported to feed on livestock. The most commonly reported deterrent for this behavior was guarding by dogs and family members.

### *Erythrocebus patas*

Sightings of *E. patas* were rare, with a total of only five encounters: Pama (1 individual); Arly (one group); Comoé (none); Koulbi (two groups); Nazinga (one group) (Tables 2 and 4). The average observed group size was 2.25 individuals, although patas were difficult to see and quick to flee. The one individual we saw in Pama was well-known to park officials and employees who reported that it had been alone for 10 years. In Koulbi, where group encounter rates were

**Figure 3.** *Galago senegalensis* observed on the edge of Pama Partial Reserve, Burkina Faso. Photo by Josh Robison.

highest, indirect observations (feeding signs) were also highest at 0.316 signs/km. *Erythrocebus patas* was reported by interviewees to occur regularly around forest edges, in agricultural zones and, while they were not observed in Comoé, they were reported to be frequent crop-feeders by villagers on the border of the AGEREF/CL park.

**Figure 4.** *Papio anubis* in Arly National Park. Photo by Josh Robison.

*Chlorocebus sabaeus and C. tantalus*

We observed *Chlorocebus* in all five reserves, for a total of 14 group encounters and an average observed group size of four (Tables 2 and 4). Only one individual was observed in Koulbi Protected Forest where interviewees reported that they were not present. Although we were unable to identify the species during the study, recent mitochondrial DNA analyses by Haus *et al*. (2013) suggest that our sightings of *Chlorocebus* in Comoé, Koulbi, and Nazinga would be of *C. sabaeus*, and in Pama and Arly *C. tantalus* (Fig. 5). Haus *et* al. (2013) did not collect fecal samples from Pama, however, or any of the land between Nazinga and Arly in Burkina, so it remains unclear where the geographic separation between these two species lies, or if hybridization is occurring at the boundary.

*Cercocebus lunulatus*

Our research team did not observe, or find signs of, *C. lunulatus* in Comoé-Léraba Partial Reserve, nor in any other location. Interviews with Comoé forest guides and farmers living in or near Folonzo, the village closest to the reserve, suggest that *C. lunulatus* may still be present though sightings are rare, even for people who frequent the forest.

**Table 1.** Primate species reported to occur in Burkina Faso, their IUCN Red List status, and the findings of our surveys. Citations in bold are of primary research; all others are secondary distribution maps.

| Species | Common name | IUCN Red List status | Listed as present in Burkina Faso by: | Presence in Burkina Faso (this study, 2012) | Conservation status in Burkina Faso |
|---|---|---|---|---|---|
| *Galagoides demidovii* | Demidoff's galago | LC – Stable | Bearder (2008); Oates (2011) | Presence not confirmed. | Status unknown. |
| *Galago senegalensis* | Northern lesser galago | LC – Stable | **Poché (1976)**: present in W National Park, SE; Bearder *et al*. (2008); Oates (2011) | Presence confirmed. | Status unknown. |
| *Cercocebus lunulatus* | White-naped mangabey | EN – In decline | **Galat and Galat-Luong (2006)**: present in Comoé-Léraba Partial Reserve, SW; Oates *et al.* (2008b); Oates (2011) | Presence not confirmed. | Highly threatened by hunting and habitat fragmentation.<br>Possibly extirpated. |
| *Papio anubis* | Olive baboon | LC – Increasing | **Poché (1976)**: present in W National Park, SE; Kingdon *et al*. (2008); Oates (2011) | Presence confirmed. | Threatened by hunting.<br>Distribution gap between Comoé-Léraba and Nazinga. |
| *Erythrocebus patas* | Patas monkey | LC – In decline | **Poché (1976)**: present in W National Park, SE; **Galat and Galat-Luong (2006)**: present in Comoé-Léraba Partial Reserve, SW; Kingdon *et al*. (2008); Oates (2011) | Presence confirmed. | Only present in small, elusive groups.<br>Extirpated from Pama Partial Reserve. |
| *Chlorocebus sabaeus* | Green monkey | LC – Stable | **Galat and Galat-Luong (2006)**: present in Comoé-Léraba Partial Reserve, SW; Kingdon and Gippoliti (2008a); Oates (2011) | Presence confirmed<br>Corroborated by **Haus et al. (2013)**: restricted to the west of the Pendjari River. | Threatened by hunting.<br>Extirpated from Koulbi Protected Forest. |
| *Chlorocebus tantalus* | Tantalus monkey | LC – Stable | Kingdon and Gippoliti (2008b); Oates (2011) | Presence confirmed<br>Corroborated by **Haus et al. (2013)**: restricted to the east of the Pendjari River. | Threatened by hunting. |
| *Colobus vellerosus* | White-thighed colobus | VU – Unknown | **Galat and Galat-Luong (2006)**: present in Comoé-Léraba Partial Reserve, SW; Oates (2011) | Presence not confirmed. | Highly threatened by hunting and habitat fragmentation.<br>Possibly extirpated. |
| *Pan troglodytes verus* | Western chimpanzee | EN – In decline | Teleki (1989): at least seasonal reports in the southwest; Redmond (2005): presence unknown; Humle *et al*. (2008): possibly extinct; Oates (2011) | Presence not confirmed. | Probably extirpated **(Ginn *et al.* 2013).** |

The last reported sighting by an interviewee was in 2010, of seven individuals along the River Comoé.

### *Colobus vellerosus*

We did not observe *C. vellerosus*, nor see any signs of its presence, in Comoé. Each of our five interviewees in or near Comoé told us that *C. vellerosus* used to be more common; three interviewees said that it had been four, 10, and 20 years respectively since they had last observed this species, and two suggested that their numbers have greatly decreased since the inception of AGEREF/CL in 1996.

**Table 2.** Signs and sightings observed for *Chlorocebus*, *Erythrocebus patas*, and *Papio anubis* across the study sites, by type, and overall encounter rates as groups per kilometer surveyed.

| Species | Study site | Sightings | Calls | Tracks | Feces | Feeding | Group encounter rate (groups/km) |
|---|---|---|---|---|---|---|---|
| *Chlorocebus sabaeus* | Comoé | 3 | - | 3 | 1 | 7 | 0.054 |
| | Koulbi | 1 | - | - | - | - | 0.021 |
| | Nazinga | 5 | - | 1 | - | 1 | 0.104 |
| *Chlorocebus tantalus* | Pama | 3 | - | - | - | - | 0.062 |
| | Arly | 3 | - | - | 1 | - | 0.060 |
| *Erythrocebus patas* | Comoé | - | - | - | - | - | * |
| | Koulbi | 2 | 2 | 5 | 2 | 15 | 0.042 |
| | Nazinga | 1 | - | 4 | 1 | - | 0.021 |
| | Pama | 1 | - | - | - | - | 0.021 |
| | Arly | 1 | - | 1 | 1 | - | 0.020 |
| *Papio anubis* | Comoé | 2 | - | 5 | 1 | 7 | 0.036 |
| | Koulbi | - | - | - | - | - | * |
| | Nazinga | 8 | 3 | 16 | 6 | 30 | 0.166 |
| | Pama | 2 | 3 | 2 | - | - | 0.042 |
| | Arly | 5 | 4 | 3 | - | - | 0.099 |

* No direct or indirect observations.

**Table 3.** Indications of poaching in each study site.

| Study Site | Direct | Camp/Stove | Gunshots | Cartridges | Traps | Tracks | Encounter rate (per km) |
|---|---|---|---|---|---|---|---|
| Pama | - | - | - | - | - | - | -* |
| Arly | - | 1 | 2 | - | - | 1 | 0.079 |
| Comoé | - | 3 | 7 | 1 | - | 5 | 0.290 |
| Koulbi | 1 | 2 | 6 | 3 | 1 | 9 | 0.443 |
| Nazinga | - | - | 1 | - | - | 2 | 0.062 |

*One *ad libitum* observation of poaching activities.

**Table 4.** Presence/absence of primates, poaching activities, and *Panthera* for each study site, and encounter rates where available. The following species were not observed nor confirmed through interviews: *Galagoides demidovii*, *Cercocebus lunulatus*, *Colobus vellerosus*, *Pan troglodytes verus*.

| Locations | *C. sabaeus* | *C. tantalus* | *E. patas* | *P. anubis* | *G. senegalensis* | *Panthera leo* | *Panthera pardus* | Poaching |
|---|---|---|---|---|---|---|---|---|
| Pama | - | P I<br>(0.062 | P I°<br>(0.021) | P S I<br>(0.042) | P I | P S<br>(0.042) | - | P*<br>(0) |
| Arly | - | P S I<br>(0.060) | P S I<br>(0.020) | P S I<br>(0.099) | I | S<br>(0.020) | S<br>(0.020) | S<br>(0.079) |
| Comoé-Léraba | P S I<br>(0.054) | - | I | P S I<br>(0.037) | I | - | S<br>(0.018) | S<br>(0.290) |
| Koulbi | P<br>(0.021) | - | P S I<br>(0.042) | - | - | - | - | P S<br>(0.443) |
| Nazinga | P S I<br>(0.014) | - | P S I<br>(0.021) | P S I<br>(0.166) | I | - | - | S<br>(0.062) |

P = Primary signs of presence (sightings); S = secondary signs (tracks, feces, feeding signs, vocalizations); I = Reported present by interviewees. Parenthetical values represent encounter rates: encounter rates for primate species are for groups encountered per km surveyed, whereas encounter rates for predators and poaching activities are signs encountered per km surveyed.

* While we report an encounter rate of zero for signs of poaching in Pama Partial Reserve, we did have one confirmation of poaching activities while we were not carrying out surveys.

° Interviewees confirmed that our sighting of one patas monkey was of a male who has been known to be the last surviving patas monkey in Pama Partial Reserve for possibly ten years.

*Poaching*

Encounter rates for signs of poaching were highest in Koulbi (0.443/km), followed by Comoé (0.290/km), Arly (0.079/km) and Nazinga (0.062/km) (Tables 3 and 4). Only one *ad libitum* sign of poaching was observed in Pama. Poaching in Burkina Faso is primarily through gun hunting; we found only one trap and no snares. We found an inverse relationship between the signs of poaching and the presence of *P. anubis* and *Chlorocebus*; namely between encounter rates for shotgun shells and encounter rates for both *P. anubis* ($r_s[5] = -0.894$, $p < 0.05$) and *Chlorocebus* spp. ($r_s[5] = -0.900$, $p < 0.05$). The presence of shotgun shells was also negatively correlated with the presence of *Panthera leo* and *P. pardus* ($r_s[5] = -0.894$, $p < 0.05$). We found no relationship between the presence of *E. patas* and encounter rates for signs of poaching. This was likely due to the low overall encounter rates for the species.

## Discussion

*Illegal Hunting*

We were only able to confirm the presence of those species considered "common and widespread," but we suggest that their distributions in Burkina Faso are patchy and relatively low, primarily due to hunting. The impact of illegal hunting of primate populations should not be underestimated (Oates 1996), and in some cases it can be more detrimental than habitat alteration and loss (Fa *et al*. 2003; Kümpel *et al*. 2008). This may be particularly true for opportunistic and omnivorous primates that more readily adapt to human habitat alteration. These species, for example *Papio* ssp. and *Chlorocebus* ssp., tend to receive little conservation attention. Even species considered to be common and widespread, however, are susceptible to local extinction; the lack of *P. anubis* and *Chlorocebus* in Koulbi Protected Forest and *E. patas* in Pama Partial Reserve may represent two such local extinctions.

**Figure 5.** *Chlorocebus tantalus* in Arly National Park, Burkina Faso. Photo by Josh Robison.

West African populations of baboons, guenons, and patas monkeys are not well-studied, affording little opportunity for comparative analyses. Encounter rates for *P. anubis* in Gashaka-Gumti, Nigeria, have been reported as 0.04–0.28 groups/km surveyed (Dunn 1993, cited by Oates 2011), and our highest encounter rates across five locations did not exceed 0.17 groups/km. This provides only one comparison, however when viewed in the context of (a) high encounter rates for signs of poaching, (b) highly limited or non-existent law enforcement or anti-poaching patrols in protected areas, (c) a strong inverse relationship between *P. anubis* and *Chlorocebus* encounter rates, and poaching activities, and (d) low and/or decreasing populations of other large mammals (for example, *Panthera leo*: Henschel *et al*. 2014 and this study; *Loxodonta africana*: Bouché *et al*. 2011 and our interviews; *Pan troglodytes verus*: Ginn *et al*. 2013), we suggest that these "common" Burkinabé primates may in fact be threatened.

The threat of hunting in Burkina Faso may not be limited to illegal hunting. Several parks, including Pama Partial Reserve, Comoé Léraba Partial Reserve (Fig. 6), and Nazinga Game Ranch and Reserve, permit legal, seasonal hunting of primates. While these were reported to be primarily opportunistic additions to hunting for larger game such as kob antelope (*Kobus kob*), these locations (except for Nazinga) tend to have little or no procedures for ongoing assessments of primate populations to ensure sustainable permit provisions. Permit hunting in reserves can be an important source of income, and in Burkina Faso, where wildlife tourism is low compared to many African nations, this funding source may be of critical importance until alternative systems such as ecotourism are developed.

Our interviews with park officials and anti-poaching patrollers revealed an overall lack in anti-poaching patrol effort and the inability of patrollers to enact the laws in place. These individuals are often placed in dangerous situations, but have been fined or even imprisoned for retaliatory action. Effective and consistent law enforcement in protected areas is vital to species' survival (Hilborn *et al*. 2006; Tranquilli *et al*. 2011; N'Goran *et al*. 2012). We recommend that the MOE implement a uniform system for assessing and managing wildlife across its protected areas (for example, incorporating data collection into anti-poaching patrols) and that anti-poaching patrollers are trained as law enforcement officials with the authority to detain and prosecute individuals.

**Figure 6.** The hands and feet of *Papio anubis* (left) found near a poaching camp (right) in Comoé-Léraba Partial Reserve, Burkina Faso. Photos by Laura Ginn.

*Crop feeding*

It is important to note that our relatively low encounter rates could be, at least in part, a reflection of primate distribution in response to agricultural expansion. Wildlife, especially those species with a proclivity toward feeding on crops, may cluster around agricultural zones and lead to low encounter rates in forest zones. Each protected area we surveyed was surrounded by agriculture, and *P*. *anubis* and *E*. *patas* were consistently reported to be avid crop feeders across the entire region surveyed. In the central and east regions, participants also reported *P. anubis* eating livestock. The most commonly stated means of preventing crop feeding was guarding, mostly by farmers or their children, and in some cases by dogs. Although trapping and/or killing were reported as methods, this was not common. Several studies have found that guarding can be effective, but the unfortunate down side to guarding is that it often falls to the children to guard, and they may be kept from school as a result (Hill 2004; Strum 2010). Guarding by adults can be just as detrimental to a family's livelihood, by keeping an individual from otherwise being productive or working for pay, and by increasing the risk of malaria by guarding at night (Hill 2004), a measure reported as necessary by participants in the villages surrounding the parks of Pama and Arly.

*Cercocebus lunulatus*

The Endangered *Cercocebus lunulatus* is likely nearing extinction in Burkina Faso. Comoé-Léraba is the only known location for the species in the country, and it was last seen in 2010 by a local guide, who reported seeing seven individuals along the river Comoé. Prior to this, the only sighting was by Galat and Galat-Luong (2006) in 2005. Interviews with guides and management revealed no other sightings of *C. lunulatus* in the park. It is possible that there is or was only one small group that migrated north from Comoé National Park (CNP) in Côte d'Ivoire (Fig. 1), where they were last reported in 2002 (Fischer *et al*. 2002). There were once plans to connect the unprotected land between CNP and Comoé-Léraba to form one large, protected area that would increase protection for the species in each reserve (Galat and Galat-Luong 2006) and provide a corridor to connect populations of animals that reside in both parks. Our interviews with AGEREF/CL revealed no plans currently underway; this leaves a 30-km gap of unprotected, unmanaged land which likely experiences heavy poaching, as do Comoé (this study) and CNP (Fischer 2004). With all populations of *C. lunulatus* experiencing high levels of fragmentation and hunting (Oates *et al*. 2000; Fischer *et al*. 2002; Gonedelé Bi *et al*. 2008; Oates 2011), the potential for safe travel between distant forest patches to maintain populations and genetic diversity is decreasing rapidly. Without a corridor connecting CNP and Comoé, and a drastic reduction in poaching in this region, the single group of *C. lunulatus* living in Comoé could be the last in the country.

*Colobus vellerosus*

*Colobus vellerosus* is in a similarly dire situation. We found no signs of *C. vellerosus* in Comoé, and interviews suggested they have been rapidly declining over the past 15 years. The last reported sighting was by a local guide in 2008. Other guides reported having not seen *C. vellerosus* for more than ten years. It is possible that their decline is due to the political unrest that began in Côte d'Ivoire in 2002; at this time, poaching in northern Côte d'Ivoire greatly increased, and decimated mammal populations in CNP (Fischer 2004). *Colobus vellerosus* only occurs in fragmented locations across Côte d'Ivoire, Ghana, Togo, and Benin (Galat and Galat-Luong 2006; Campbell *et al*. 2008; Oates 2011) and is susceptible to hunting (Refisch and Koné 2005). Vocalizations of both *C. vellerosus* and *C. lunulatus* have recently been heard in CNP, Côte d'Ivoire (K. Linsenmair, pers. comm.). After several years without active research or law enforcement, and heavy poaching, this is evidence of their resilience. This population should be investigated further and, with increased protection along the border of Côte d'Ivoire, these species may be able to extend and survive in Burkina Faso.

## Conclusion

We have confirmed the presence of *Galago senegalensis, Papio anubis*, *Erythrocebus patas*, *Chlorocebus sabaeus* and *C. tantalus* in Burkina Faso. We were unable to confirm the presence of *Galagoides demidovii, Cercocebus lunulatus*, *Colobus vellerosus*, and *Pan troglodytes verus* (see Ginn *et al.* 2013). If small populations of *Cercocebus lunulatus* and *Colobus vellerosus* remain in southwestern Burkina Faso, they are highly threatened by hunting and habitat loss and degradation. Like chimpanzees, they are either already extirpated or nearing extirpation from the region. More in-depth surveys are needed to determine the actual abundance of primates and contribute to the regional distribution information for large-scale species monitoring. We recommend that, in the forests where anti-poaching patrols are regularly conducted such as Nazinga, patrol units are trained in data collection techniques in order to combine anti-poaching patrols and reconnaissance surveys to maintain encounter rates for all mammal species that can be monitored over time, and to ensure that legal hunting practices are not negatively impacting primate populations. Studies of the human-wildlife interactions in Burkina Faso, and in ways to mitigate the effects of human-wildlife conflict, are necessary to alleviate the negative effects of agricultural expansion for both humans and non-human primates as human populations increase.

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# Trade in Bengal Slow Lorises in Mong La, Myanmar, on the China Border

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**Abstract:** Despite being protected throughout their range, the illegal trade in slow lorises is a clear impediment to their conservation. Little is known about this trade from Myanmar. We report on three visits to the town of Mong La, Myanmar, on the border with China, where Bengal slow lorises *Nycticebus bengalensis* are traded illegally. Combined with survey data from other researchers, it is clear that slow lorises are ubiquitously present at Mong La's animal market. They are traded either as parts—carcasses, skins, and hands and feet (average of 26 items/survey)—or alive (average of 5 individuals/survey). Live animals typically arrive at the market in the morning; they are slaughtered, and the carcass at least is sold the same day. Estimating from live animals, our data suggest that over a thousand Bengal slow lorises may be traded annually from this one market alone. Trade in Mong La may be local or may be geared towards the Chinese market, and thus the trade in Mong La is not only contra to Myanmar's law but also clearly violates the rules and intentions of CITES. We hope that by documenting the trade in slow lorises we will raise awareness amongst conservationists and primatologists about the realities of the unsustainable hunting of slow lorises and that it will be an incentive for the Myanmar and Chinese authorities to take appropriate action to curb this illegal trade.

**Key words:** Slow loris, *Nycticebus*, Burma, wildlife trade, CITES, conservation

## Introduction

The Bengal slow loris *Nycticebus bengalensis* has the northernmost range of all of the slow lorises. It is distributed from Bhutan and Northeast India in the west to southern China and Vietnam in the east, and south to the Thai-Malay Peninsula. Individuals in the northern part of this range appear to be the largest of the slow lorises, with a head-body length of up to 38 cm and weighing up to 2100 g (Nekaris 2013). The Bengal slow loris, listed as Vulnerable on the IUCN Red List (Streicher *et al*. 2008), is threatened in part by habitat loss and fragmentation, but it is becoming increasingly clear that in fact commercial wildlife trade poses the greatest threat. In the early 1990s, Wang *et al.* (1996) recorded Bengal slow lorises in the markets of the Chinese border towns of Ruili (~65 individuals), Longchuan (~60 individuals), and Daluo (2 individuals), allegedly all from Myanmar, and in Meng La (~40 individuals), allegedly from Laos. Starr *et al*. (2010) reported on the trade in Bengal slow lorises in Cambodia, and Osterberg and Nekaris (2015) in Thailand. Three studies concur that wildlife trade in the Northeast Indian states of Meghalaya, Assam, Arunuchal Pradesh and Nagaland is a severe threat to the species (Radhakrishna *et al*. 2006; Nandini *et al*. 2009; Das *et al*. 2014). Nekaris *et al*. (2010) concluded that of all the slow lorises, the Bengal slow loris and the pygmy slow loris *N. pygmaeus* were the species most traded internationally for their body parts. There are numerous other reports of slow lorises in trade within the range of Bengal slow lorises, but not all of them make it explicit whether it is the Bengal slow lorises or, for instance, the sympatric pygmy slow lorises, that are involved (e.g., Wenjun *et al*. 1996; Martin and Phipps, 1996; Lau *et al*. 1997; Li and Wang 1999).

Here we report on trade in Bengal slow lorises in the town of Mong La in Myanmar, on the border with China, based on spot checks. We show that slow lorises were present during all surveys, with a high turnover, to the effect that thousands of individuals are killed annually to supply the demand from this one market alone.

## Methods

### *Study area*

Mong La is a small town situated in 'Special Region 4' in Shan State in eastern Myanmar on the border with China.

Special Region 4 is controlled by Sai Leung (also known as Lin Min Xiang) and is policed by the 3,000-strong National Democratic Alliance Army of the Eastern Shan State that enforces its own set of laws (Oswell 2010); the Myanmar central government have limited authority in Mong La. Mong La's position on the border with China's Yunnan Province facilitates cross-border trade. Starting in June 1989, when Special Region 4 was granted virtual autonomy, the town was developed by Chinese investors and focuses on the entertainment industry, with numerous nightclubs, brothels, exotic meat restaurants, and 24-hour casinos (Davies 2005). About 80% of the people working and living in the area are Chinese. Chinese is spoken widely in Mong La, Chinese writing is omnipresent, the mobile phone network and electricity providers are Chinese, and the Chinese Yuan Renminbi, and not the Myanmar Kyat, is the currency of daily use. Local time follows Beijing Standard Time and is 1.5 hours ahead of the rest of Myanmar.

Wildlife is traded in three distinct ways in Mong La (Shepherd and Nijman, 2007; Felbab-Brown, 2011; Nijman and Shepherd, 2014): first, specialized permanent wildlife shops are spread out over the town, selling ivory, wild cat skins, trophies, etc.; second, the morning market in the central town square sells a combination of live or freshly killed animals and dried animal products; and third, a row of some 15 restaurants sell wild meat, displaying live animals in cages and tubs on the street in front of the restaurants.

**Figure 1.** Illegal trade in Bengal slow lorises *Nycticebus bengalensis* at Mong La market, Myanmar, January 2014. From top left, clockwise: day 1, slow loris in cage; slow loris being taken apart; slow loris carcasses and skin drying in the sun; day 2, slow loris fur for sale amongst a variety of other wildlife. Photos by Vincent Nijman and Chris R. Shepherd.

### *Data acquisition*

VN and CRS visited the morning market on four occasions; 7 February 2006, 28 February 2009, and 1 and 2 January 2014. All slow lorises and their parts were counted, apart from a second round during the last visit when only alive and freshly killed individuals were counted (so as not to double count). We visited the market in the early morning when the animals had just arrived; on 1 January 2014 we revisited the market in the afternoon when trading was no longer active to check what was still on display. On the same days we surveyed wildlife trade shops and the wild meat restaurants. In addition we collected data on the trade in slow lorises by searching for reports from others that have visited Mong La in recent years.

## Results

We observed Bengal slow lorises for sale at two locations; in shops surrounding the town's central square and in the morning market. Others have observed them in front of the exotic meat restaurants on the south side of the river (see below). They are traded for their meat (to the wild meat restaurants) but more commonly for body parts used for traditional Asian medicine.

During the 2007 survey, we observed two live slow lorises, each housed in a single cage, five skins, four hands and feet, and two whole, fresh skeletons—a minimum of seven individuals. All were found in the morning market. In the 2009 survey, we observed 19 skins, 10 whole fresh skeletons, four feet, one skull and two live individuals—a minimum of 21 individuals. One dealer charged CNY 300 (US$50) for each live slow loris, although it was being offered to a Caucasian foreigner and the price was probably inflated. During the 1 January 2014 survey we observed 15 live slow lorises in the morning market, housed singly in cages, in pairs or up to four individuals per cage. We found four slow lorises that had been killed the same morning. Twelve hands and feet, presumably of three slow lorises were on display, as were the skins of four additional lorises. No live slow lorises were on sale when we returned to the market in the afternoon, but eight freshly skinned slow lorises were laid out on cardboard to dry. In the survey next morning, we observed four live slow lorises in cages and six that were freshly killed. One vendor was in the process of skinning a loris she had just killed. One shop had two live slow lorises in a cage, observed on the second day, and another shop displayed eight hands and feet.

A documentary "The Mong La Connection," shot in Mong La in 2006 (www.cultureunplugged.com/storyteller/Karl__Ammann#/myFilms) shows two skins, two skeletons, and three live slow lorises for sale at the morning market (see also Peterson 2007). On 18 April 2008, Danny Benovitch visited the morning market and meat restaurants in Mong La and posted 91 photographs on his Flickr page; it is clear that at least four Bengal slow lorises, alive in cages, were on display, on that day, including three in front of the exotic meat restaurants. Seamus Martov (in litt. 2014) visited Mong La in January 2014 and found slow lorises for sale in the town and two live individuals in a cage in the morning market. Sebastian Strangio (in litt. 2014) visited Mong La in May 2014 and photographed at least six skins and six carcasses for sale in the morning market. Adam Oswell (Oswell 2010; in litt. 2014), who has visited Mong La nine times since 2001, recalled the presence of slow lorises during all visits but did not record enough details for us to quantify the numbers in trade.

## Discussion

We observed seven, 21, 22 and 12 slow lorises, either whole or in parts, during the four surveys of Mong La. Others have observed minimum numbers of six, five, four and three, respectively. Slow lorises are evidently ubiquitous in Mong La's animal market.

It is clear that slow lorises are not normally kept alive for more than 24 hours in the market and are either sold alive on the morning of their arrival or are killed and skinned later that day. We found no storage facilities on site, and all other perishable wildlife is treated in the same manner. This practice is quite different from many other markets where we have monitored the trade in slow lorises, such as Indonesia, where they are kept alive for longer periods of time and most often sold as pets, or Cambodia where mainly skins have been observed but not live animals entering the market (Nekaris *et al*. 2010; Shepherd 2010; Starr *et al*. 2010). With this in mind, and considering only live and freshly killed individuals, it seems that between two and nineteen (and on average eight) slow lorises are killed and processed at this market per day. If our observations are indicative to what happens on other days—and we have no reason to believe this is not the case—the annual turn-over of Bengal slow lorises at this one market alone must be measured in the thousands of individuals. An annual turn-over of one thousand slow lorises requires that just under three lorises need to be killed a day; this is less than was observed on any of the days we were present. Just over five lorises killed per day would indicate two thousand sacrificed per year for the trade in this town.

It is worthwhile recalling the slow life history of Bengal slow lorises. As summarized by Nekaris (2013), the earliest that males and females start to reproduce is at the age of about 18 months, gestation lasts some six months, and females lactate for six months (during which time conception is presumably delayed). With only one offspring born at a time, this slow rate of reproduction is incompatible with the high rate of capture by hunters.

Bengal slow lorises are protected under Myanmar law, and international trade in slow lorises is prohibited as the entire genus is listed in Appendix I of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES), to which both Myanmar and China are signatories (Nekaris and Nijman 2007). Trade in Mong La is geared toward the Chinese market (Shepherd and Nijman 2007) and thus the trade in Mong La is not only illegal under Myanmar law but also clearly violates the rules and intentions of CITES. We hope that documenting the trade in slow lorises raises awareness amongst conservationists and primatologists about the realities of this trade and that it will be an incentive for the Myanmar and Chinese authorities to take appropriate action to curb it.

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# Distribution and Current Status of the Capped Langur *Trachypithecus pileatus* in India, and a Review of Geographic Variation in its Subspecies

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**Abstract:** In India, the capped langur (*Trachypithecus pileatus*) occurs in Assam, Arunachal Pradesh, Manipur, Meghalaya, Mizoram, Nagaland, and Tripura. Elsewhere it is found in Bhutan, Bangladesh, northwestern Myanmar and a small area of Tibet, China. It is a forest-dwelling primate occurring in lowland, wet, evergreen rain forest to temperate forest. It ranges from the plains, 5 m above sea level, to 2,800 m in the Himalaya. Although it is the second most abundant primate of Assam, its populations are declining due to continuous destruction of its forests, and also hunting. Since the 1980s, one-third of the capped langur habitat in Assam has been lost because of tree felling and encroachment. It has been recorded in 53 protected areas in Northeast India. Of five subspecies recognized in the past (*pileatus, durga, brahma, shortridgei* and *tenebricus*) *shortridgei* is now considered to be a full species, and *durga* a junior synonym of *pileatus*. *Trachypithecus p. pileatus* occurs south of the Brahmaputra River; *T. p. brahma* and *T. p. tenebricus* occur north of the river. The lower reaches of the Jia-Bhoreli–Kameng River separate *tenebricus* (in the west) from *brahma* (in the east), but in the upper reaches in the higher Himalaya there is possible intergradation. Here, I report on hitherto unrecorded differences in facial hair patterns (especially the cap) that differentiate the three subspecies. The langurs south of the Brahmaputra (*pileatus*) have shorter whiskers, and a distinct, conspicuous "army-cut hairstyle"-like cap, well separated from the ears. The subspecies to the north can be separated by the form of the cap—hairs radiating from the forehead to form a shaggy cap in *tenebricus*, and a less shaggy cap, resembling that of *pileatus*, but which extends to the ears in *brahma*. The distinguishing features are more dependable than overall color patterns, which vary individually and with age, sex, and season.

**Key Words:** Capped langur, *Trachypithecus pileatus*, distribution, geographic variation.

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## Introduction

In India, the capped langur, *Trachypithecus pileatus* (Blyth, 1843), occurs in the northeastern states of Assam, Arunachal Pradesh, Manipur, Meghalaya, Mizoram, Nagaland, and Tripura (Choudhury 1989b, 2013). Elsewhere, it extends into Bhutan (Choudhury 1990c), Bangladesh (Khan 1981), northwestern Myanmar (west of the Chindwin River), and a small area of Tibet, China (Choudhury 2012, 2013; Groves 2001; Groves *et al*. 2013).

Five subspecies have been recognized—*Trachypithecus p. pileatus* (Blyth, 1843), *T. p. durga* (Wroughton, 1916), *T. p. brahma* (Wroughton, 1916), *T. p. shortridgei* (Wroughton, 1915), and *T. p. tenebricus* (Hinton, 1923) (see Pocock 1939; Ellerman and Morrison-Scott 1951). The subspecies *shortridgei* was upgraded to a full species by Groves (2001, 2005; see also Groves *et al.* 2013), and *durga* is now considered to be a synonym of *pileatus* (see Choudhury 2012, 2013). The ranges of three subspecies, *pileatus*, *brahma*, and *tenebricus*, are separated by the wide Brahmaputra River and its tributary, the Jia-Bhoreli. *Trachypithecus p. pileatus* occurs to the south of the Brahmaputra, and *T. p brahma* and *T. p. tenebricus* to the east and west of its northern tributary, the Jia-Bhoreli River, respectively. There is no barrier, however, between *brahma* and *tenebricus* in the upper reaches of the Jia-Bhoreli–Kameng (in the higher Himalaya), and there are possible intergrades.

The capped langur is found in tropical, wet, evergreen rain forest (annual rainfall above 3,000 mm, and in places exceeding 10,000 mm) to moist, deciduous forest (annual rainfall often less than 900 mm). It ranges from the low plains (10 m above sea level in Tripura, but as low as 5 m in Bangladesh) to 2,800 m in Nagaland and the eastern Himalaya (there is an extreme record at 3,000 m in temperate forest, near Thungri, West Kameng district in Arunachal Pradesh) (Choudhury 2012, 2013). In the high mountains, groups show seasonal altitudinal movements that are governed by snowfall. They move up the slopes in summer, and return to the middle slopes in the winter.

Although the capped langur is the second most abundant primate in Assam, it is declining due to the continuous destruction of its habitat and hunting. At least one-third of the capped langur's habitat in Assam has been lost since the 1980s because of tree felling and encroachment.

Until the mid-1980s, the scanty literature available for *T. pileatus* was restricted to publications by Hinton (1923), Pocock (1928), McCann (1933, 1942), Oboussier and Maydell (1959) and Khajuria (1962), with some information also provided by Blanford (1888–1891), Finn (1929), Prater (1948), Ellerman and Morrison-Scott (1951), Napier and Napier (1967), Roonwal and Mohnot (1977), and Khan and Ahsan (1981). Hinton (1923) and Pocock (1928) gave detailed accounts on taxonomic variation; the others provided general information, including characteristics, distribution, and aspects of their ecology and behavior. Subsequent studies carried out in Northeast India are reported in Choudhury (1988, 1989a, 1990b, 1990c, 1992a, 1993, 1996b, 1997a, 1996b; mainly in Assam but also other states); Borang and Thapliyal (1993; in Arunachal Pradesh); Mukherjee and Chakraborty (1992; in Tripura), Mishra *et al.* (1994; in Mizoram), and Kumar and Solanki (2008; in Arunachal Pradesh). Choudhury (1989b, 1990a) and Kumar (2006) studied their ecology and behavior. General information on capped langurs, including their distribution in Bhutan, is provided by Choudhury (1990c, 2008a) and Wangchuk *et al*. (2004). Gittins and Akonda (1982) and Ahsan (1994) reported on capped langurs in Bangladesh. Stanford (1989, 1991) carried out in-depth studies on their ecology and behavior in Bangladesh (see also Kabir and Islam 1994). A detailed review covering various aspects of capped langur biology and conservation is found in Choudhury (2012), and mapping with further updates in Choudhury (2013).

Here, I review the information available from my surveys and those of others reported in the published literature to better describe the geographic ranges of the three subspecies and, using photography backed up by the examination of specimens in a number of museums and collections, I describe hitherto unrecorded differences in facial hair patterns, especially the cap, to clarify further the differences between the subspecies. The langurs south of the Brahmaputra (*pileatus*) show a conspicuous "army-cut hairstyle"-like cap. While the earlier segregation was based on pelage color that was always somewhat confused due to significant seasonal color variations, the new features added in this study do not change with season, making them more comprehensible and consistent than the earlier characteristics used.

## Methods

Mammal surveys, carried out in different parts of Northeast India since the early 1980s, have provided information on the distribution and status of the capped langur (Choudhury 1982, 1986, 1992b, 1997a, 2001, 2002a, 2008a). I have travelled widely in Assam, Arunachal Pradesh, Meghalaya, Manipur, Mizoram, Nagaland and Tripura, and also visited Bhutan, Bangladesh and Myanmar (Choudhury 2013). At times, specific survey projects on primates were also undertaken; for example, between 1986 and 2000 (Choudhury 1989a, 1995, 1996a, 1997b).

I carried out an extensive literature search when compiling entries for *Mammals of South Asia* (Choudhury 2012 in Johnsingh and Manjrekar 2012) and also when writing *The Mammals of North-East India* (Choudhury 2013). In 2001, I examined specimens in the following museums: the National Museum of Natural History, Smithsonian Institution, Washington DC; the American Museum of Natural History, New York; the Field Museum of Natural History, Chicago; and the Museum of Vertebrate Zoology, Berkeley, CA. I also visited collections of the Zoological Survey of India (Kolkata, Shillong and Itanagar); the Bengal Museum of Natural History, Darjeeling; Itanagar Museum; Museums of the Forest Department at Shillong and Guwahati; the Museum of the Bombay Natural History Society; the collection of the Forest Museum of Project Tiger at Miao, near Namdapha National Park; the Assam State Museum, Guwahati; Kohima Museum, Nagaland; and the State Museum, Itanagar.

I photographed as many langurs as I could to examine variations in pelage in Assam (since 1983), Arunachal Pradesh (since 1989), Manipur (since 1988), Meghalaya (since 1995), Mizoram (since 1987), and Nagaland (since 1991). Some photographs were provided by other photographers; they are listed in the acknowledgements. Cameras used were Canon T50, Nikon FM2, D5100 with telephoto and telezoom lenses, and Lumix FZ28.

## Results

### Distribution

The capped langur is found throughout a large part of the states of Assam, Arunachal Pradesh, Manipur, Meghalaya, Mizoram, Nagaland, and Tripura, both north and south of the Brahmaputra River. It is not found to the west of the Manas River—there, it is replaced by the golden langur *Trachypithecus geei*—and between the Siang and Dibang rivers. It has been recorded in 53 protected areas, and it may occur in three more, but this has yet to be confirmed. Elsewhere, it occurs in eastern Bhutan, Bangladesh, north-western Myanmar (west of Chindwin River), and in a small part of Tibet (west of the Yarlung Zangbo; George B. Schaller, pers. comm., seen in 2001; Appendix 1). The distribution of *T. pileatus* is shown in Figures 1 and 2. The distribution in each of the Indian states is described below. Protected areas having capped langurs are listed in Table 1.

***Arunachal Pradesh.*** The capped langur occurs in all the districts west of the Siang River and east of the Dibang River. Strangely, no langurs occur in the tract between these two rivers; a finding also confirmed by Borang and Thapliyal (1993). Outside the protected areas, there are sizeable

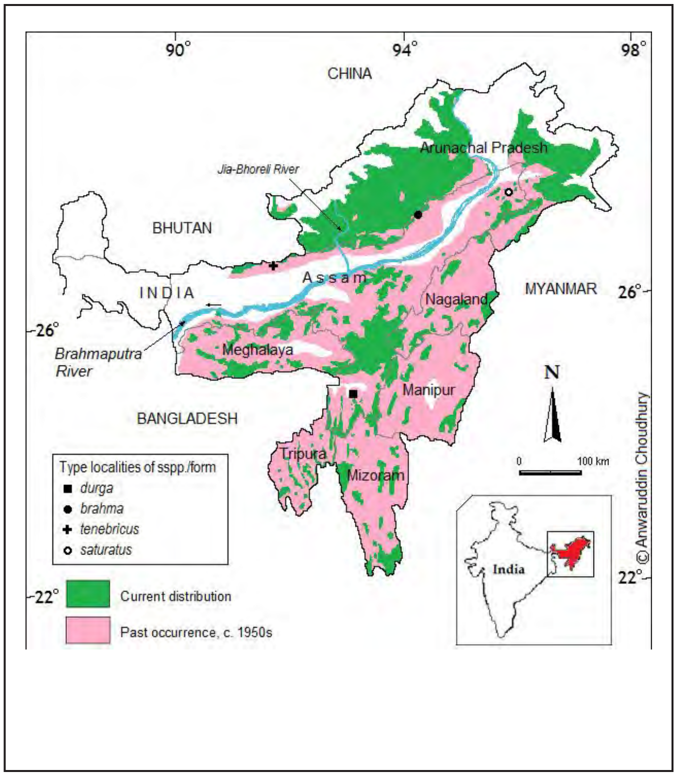


**Figure 1.** The past and present distribution of the capped langur, *Trachypithecus pileatus*, in India. Adapted from Choudhury (2013) with some changes, viz. the Jia-Bhoreli River, and the type localities of *T. p. durga* (Wroughton, 1916), *T. p. brahma* (Wroughton, 1916), *T. p. tenebricus* (Hinton, 1923), and *T. p. saturatus* (Hinton, 1923). Map drawn by Anwaruddin Choudhury.

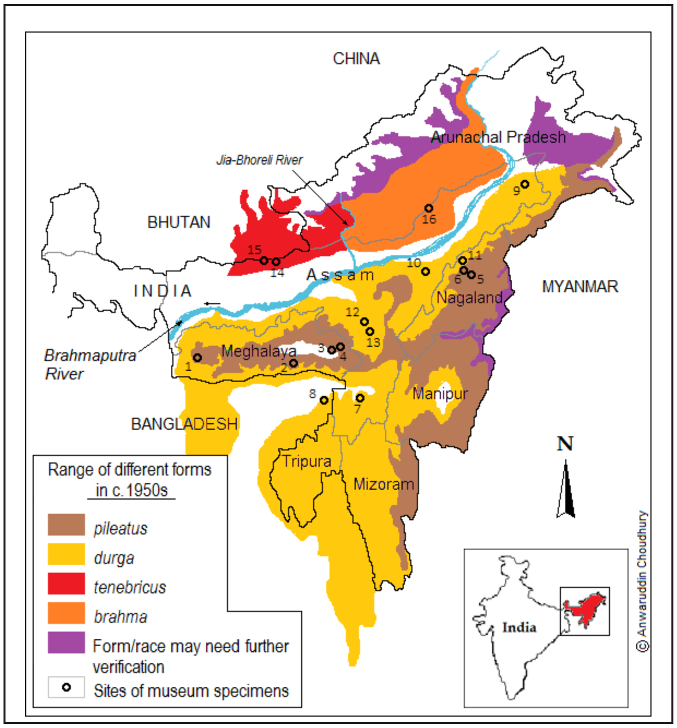


**Figure 2.** North-East India and adjacent areas of Bhutan, Bangladesh and China (Tibet) showing the ranges of the different forms in the 1950s, with museum specimen locations. For reference to the sites and specimens, see Hinton (1923) and Pocock (1928). The sites are: 1. Tura; 2. Laitkynsew; 3. Raliang, 4. Khonshnong; 5. Mokokchung; 6. Chongliyemsem; 7. Cachar; 8. Sylhet; 9. Bar Hapjan; 10. Golaghat; 11. Lakhuni; 12. Lanka; 13. Lamsakhang; 14. Motonga River; 15. Menoka Nadi; and 16. Siajuli. Map drawn by Anwaruddin Choudhury.

populations in some of the reserved forests, such as Doimara, Amortola, Manabhum, Talle, Tengapani and Papum. The largest contiguous tracts of habitat are also found in this state (Fig. 1). There are still large tracts in relatively remote areas where the langur is likely to hold its ground in the decades to come. However, in easily accessible areas it is declining (except in the west, especially Tawang and higher West Kameng, where the influence of Buddhism means that there is little hunting).

***Assam.*** The capped langur is found in all the districts within its range to the north and south of the Brahmaputra River. Although its known western limit is the Manas River, in the north, there are a few reports of capped langurs from Bhairab Pahar and Kabaitari Tilla (near Jogighopa) in the Bongaigaon district (formerly the undivided Goalpara district), to the west of the river (the late Mohd. Moosa, pers. comm. 1988). It is more common than the Rhesus macaque *Macaca mulatta* in forested areas. The districts which are outside its range are Bongaigaon, Chirang, Dhubri (north bank), and Kokrajhar—all part of a formerly undivided Goalpara, and all have the golden langur (*Trachypithecus geei*)—and Barpeta, Nalbari and Darrang. It still occurs in the remaining 20 districts. It has vanished from most of the plains of the Brahmaputra valley. Unlike the other states where hunting was the key factor for its decline, in Assam it is mainly habitat loss and organized encroachment. Outside the protected areas there is sizeable habitat in the Dhansiri, Inner Line, Joypur, Katakhal, Langting–Mupa, Lumding, and Upper Dihing (east and west blocks) reserved forests. The largest that has suitable habitat is in the district of Karbi Anglong. A small population of langurs frequent the Panjabari area of Guwahati city where they come from the fringe of the Amchang Sanctuary. Other populations in the hillocks of Guwahati city were extirpated in the 1980s.

***Manipur***. The capped langur is mainly confined to five hill districts (Chandel, Churachandpur, Senapati, Tamenglong, and Ukhrul) and the Jiribam subdivision of Imphal East district. In the Manipur valley proper it is no longer found. Outside the protected areas there are sizeable forest patches in the Tolbung reserved forest and Moreh proposed reserved forest. There is a specimen (male) in the Zoological Survey of India from Kalanaga, Barail Range in Senapati district, which was obtained in 1936.

***Meghalaya***. The capped langur is patchily distributed in all the districts. South Garo Hills, Ri-Bhoi and East Jaintia Hills districts are the main areas, having the largest forests where the capped langur is still present. There is sizeable habitat in Narpuh (blocks I and II) reserved forests in East Jaintia Hills district, Nongkhyllem reserved forest in Ri-Bhoi district, and in the private and community forests of West and Southwest Khasi Hills districts.

***Mizoram***. Overall the capped langur is still widespread. It has been recorded in all the districts. Outside protected areas there are scattered populations in the Inner Line, Tut Lungkaih, Puankhai and Ngengpui reserved forests, and also in forests in the extreme south, covering the southern parts of Lunglei, Lawngtlai and Saiha districts. Populations otherwise are small and scattered.

***Nagaland***. Although the langur has vanished from many areas, scattered groups still occur in all the districts. It is doubtful that any survive in Pulie Badge Wildlife Sanctuary near Kohima town. It has been extirpated from Rangapahar Wildlife Sanctuary near Dimapur. Capped langurs occur in the mountain range along the India–Myanmar border, including Saramati and Noklak where some good habitat can still be found. In Saramati, it occurs at elevations up to 2,800 m. There are three specimens in the American Museum of Natural History from Changchang Pani, Mokokchung district that were obtained by Charles McCann in 1930.

***Tripura***. Capped langurs were recorded in all the districts. However, its range is no longer contiguous and is heavily fragmented. Most langurs are now found in the low hills, as the plains areas have come under human occupation. There are still scattered groups outside the protected areas.

### *Status*

*Trachypithecus pileatus* is the most common langur of Northeast India. It is the second most abundant primate in Assam after the Rhesus macaque (Choudhury 1989a, 1996b). In Arunachal Pradesh it is the second most abundant species after the Assamese macaque *Macaca assamensis*. Populations, however, are declining everywhere. Capped langurs are common in the forests of Assam and Arunachal Pradesh but, due to hunting, not in Manipur, Meghalaya, Mizoram, Nagaland and Tripura. In Arunachal Pradesh the species is particularly common in some areas, especially where it is not molested, such as in Tawang and West Kameng districts. Unlike these parts of Assam, in other states hunting means that any isolated group or few remnant individuals have little chance of survival.

**Table 1.** Protected areas with known populations of *T. pileatus*.

| Name of the protected area | Area (km²) | Subspecies |
|---|---|---|
| **Assam** | | |
| Amchang Wildlife Sanctuary | 78.64 | *pileatus* |
| Barail Wildlife Sanctuary | 326.25 | *pileatus* |
| Bherjan–Borajan–Podumoni Wildlife Sanctuary | 7.2 | *pileatus* |
| Bornadi Wildlife Sanctuary | 26.2 | *tenebricus* |
| Dibru–Saikhowa National Park | 340.0 | *pileatus* |
| Dihing–Patkai Wildlife Sanctuary | 111.19 | *pileatus* |
| East Karbi Anglong Wildlife Sanctuary | 221.8 | *pileatus* |
| Garampani Wildlife Sanctuary | 6.0 | *pileatus* |
| Hollongapar Gibbon Sanctuary | 20.0 | *pileatus* |
| Kaziranga National Park | 473.0 | *pileatus* |
| Laokhowa Wildlife Sanctuary | 70.0 | *pileatus* (nearly extirpated) |
| Manas National Park | 500.0 | *tenebricus* |
| Marat Longri Wildlife Sanctuary | 451.0 | *pileatus* |
| Nambor Wildlife Sanctuary | 37.0 | *pileatus* |
| Nambor–Doigrung Wildlife Sanctuary | 97.1 | *pileatus* |
| Nameri National Park | 200.0 | *brahma, tenebricus* (latter just outside, W of the river in Potasali) |
| North Karbi Anglong Wildlife Sanctuary | 96.0 | *pileatus* |
| Sonai–Rupai Wildlife Sanctuary | 220.0 | *tenebricus* |
| **Arunachal Pradesh** | | |
| Eagle's Nest Wildlife Sanctuary | 217.0 | *tenebricus* |
| Itanagar Wildlife Sanctuary | 140.0 | *brahma* |
| Kamlang Wildlife Sanctuary | 783.0 | *pileatus* |
| Kane Wildlife Sanctuary | 31.0 | *brahma* |
| Mehao Wildlife Sanctuary | 281.5 | *pileatus* |
| Mouling National Park | 483.0 | *brahma* |
| Namdapha National Park | 1985.0 | *pileatus* |
| Pakke Wildlife Sanctuary | 862.0 | *brahma* |
| Sessa Orchid Sanctuary | 100.0 | *tenebricus* |
| Talle Wildlife Sanctuary | 337.0 | *brahma* |
| Yordi Rabe Supse Wildlife Sanctuary | 397.0 | *brahma* |
| **Nagaland** | | |
| Intanki National Park | 202.0 | *pileatus* |
| Fakim Wildlife Sanctuary | 6.4 | *pileatus* |
| **Manipur** | | |
| Bunning Wildlife Sanctuary | 115.0 | *pileatus* |
| Jiri–Makru Wildlife Sanctuary | 198.0 | *pileatus* |
| Kailam Wildlife Sanctuary | 187.0 | *pileatus* |
| Yangoupokpi Lokchao Wildlife Sanctuary | 184.0 | *pileatus* |
| Zeilad Lake Wildlife Sanctuary | 21.0 | *pileatus* |
| **Mizoram** | | |
| Dampa Wildlife Sanctuary | 480.0 | *pileatus* |
| Khawnglung Wildlife Sanctuary | 35.75 | *pileatus* |
| Lengteng Wildlife Sanctuary | 60.0 | *pileatus* |
| Murlen National Park | 100.0 | *pileatus* |
| Phawngpui National Park | 50.0 | *pileatus* |
| Pualreng Wildlife Sanctuary | 50.0 | *pileatus* |
| Ngengpui Wildlife Sanctuary | 110.0 | *pileatus* |
| Tawi Wildlife Sanctuary | 35.0 | *pileatus* |
| Thorangtlang Wildlife Sanctuary | 198.0 | *pileatus* |
| Tokalo Wildlife Sanctuary | 250.0 | *pileatus* |
| **Tripura** | | |
| Gumti Wildlife Sanctuary | 389.5 | *pileatus* |
| Sepahijala Wildlife Sanctuary | 18.5 | *pileatus* |
| Trishna Wildlife Sanctuary | 170.6 | *pileatus* |
| **Meghalaya** | | |
| Balpakram National Park | <200.0 | *pileatus* |
| Nokrek National Park | 68.0 | *pileatus* |
| Noghkhyllem Wildlife Sanctuary | 29.0 | *pileatus* |
| Siju Wildlife Sanctuary | 5.2 | *pileatus* |

**Table 2.** Differences between three subspecies of *Trachypithecus pileatus*.

| **Subspecies** | ***pileatus*** | | ***brahma*** | | ***tenebricus*** | |
|---|---|---|---|---|---|---|
| Synonyms | ***durga*, *argentatus*, *saturatus*** | | | | | |
| | W | D | W | D | W | D |
| Gray cap extends to the ear | – | | + | | + | |
| Side of cap has 'army-cut' 'hair'-style look | + | | – | | – | |
| Cap generally shaggy | – | | Less shaggy | | + | |
| Hair on the cap/crown are laid straight or nearly so from the forehead | + | | + | | – | |
| Hair on cap/crown radiates from forehead and other points | – | | – | | + | |
| Hairs on both sides of head (cap) gives a 'horny' look | – | | + | | + | |
| Side whiskers very long extending much beyond ears | – | | + | | + | |
| Side whiskers long extending just beyond ears | + | | – | | – | |
| Whitish tufts on point of ears (like *T. shortridgei* but shorter) | – | | + | | + | |
| Dark dorsum narrower | + | | –/+ | | – | |
| Seasonally lower part of dorsum and flanks has lot of yellowish and/or paler | + | | + in western animals (in Pakke)<br>– in eastern animals | | – | |
| Dorsum | Gray or brownish gray | Gray. Darker in eastern areas | Darker gray (lighter than in wetter months) | Darker gray | Dark gray | Very dark gray |
| Dorsum: lower part | Gray or brownish gray | Gray with yellow | Darker gray (lighter than in wetter months) | Darker gray with reddish-yellow | Darker gray (lighter than in wetter months) | Very dark gray with small reddish areas marginally |
| Ventrum: upper part | Yellowish buff or light yellowish orange | Golden yellow or yellowish orange | Buff white | Buff white with some orange | Buff to creamy | Reddish or orange red |
| Ventrum: lower part (abdomen) | Yellowish buff or light yellowish orange but lighter | Golden yellow or yellowish orange but lighter | Buff white | Buff white but with less orange | Lighter; mostly buff to creamy with faint red | Lighter; mostly buff to creamy with no or little red |
| Cheek whiskers | Yellowish buff | Yellowish orange | Buff and light gray | Buff | Buff and light gray | Orange buff and light gray |

+ Present; – Absent; D = drier seasons (c. November/December to March/April; such coat color may be seen also up to May in some animals); W = wetter seasons (c. April/May to October/November).

At least one-third of the capped langur's habitat in Assam has been lost since the 1980s due to felling and encroachment. Reserved forests such as Balipara, Charduar, Naduar and Biswanath in Sonitpur district, all prime habitat of the langur till the mid-1990s, have lost almost 90% of their forests for the same reasons (Choudhury 2002b). Likewise, the reserved forests of Upper Dihing (west block) in Tinsukia district, Inner Line in Cachar and Hailakandi districts, and Nambor (north block) in Golaghat district have been reduced by 50% since 1980. The entire habitat and langur populations of some reserved forests in Assam such as Gohpur, Gali, Nambor (south block), Diphu, Doyang and Rengma vanished in the 1970s and 1980s. In Meghalaya and Nagaland, and the hill areas of Manipur, Mizoram and Tripura, only the protected areas still have reasonable populations of capped langurs that have otherwise become scattered, scarce and locally extirpated in many areas because of *jhum* cultivation and hunting. Despite excellent habitat, in some parts of Arunachal Pradesh they are now very rare or locally extirpated due to hunting for their skins, used by some tribes in making traditional *dao*-sheaths (the *dao* is a long knife).

### *Geographic variation*

Five subspecies or races used to be recognized (Hinton, 1923; Pocock 1939; Ellerman and Morrison-Scott 1951): *pileatus, durga, brahma, tenebricus* and *shortridgei*. *Trachypithecus shortridgei*, which occurs in northern Myanmar and extreme western Yunnan (China), was upgraded to a species (Groves 2001, 2005; Groves *et al.* 2013). *Trachypithecus p. brahma* and *T. p. tenebricus* are found north of the Brahmaputra River and west of the Siang River, *T. p. durga* and *T. p. pileatus* occur south of the river (Choudhury 1994, 1997a).

Choudhury (1997a) recommended that a fresh review is needed in view of seasonal variations in pelage color and of observations in the wild of individuals with characteristics of two or even three races in the same area and even in the same group. Choudhury (2013) recognized just three subspecies, considering *durga* Wroughton, 1916, to be a synonym of *pileatus* owing to insignificant color variation and their occurrence in the same geographical area without any barrier (Table 2). As such. populations south of the Brahmaputra are now considered to belong to just one subspecies; *pileatus* Blyth, 1843.

Further studies, including extensive photography, have provided new insights. The subspecies *brahma* and *tenebricus*, both to the north of the Brahmaputra, have features in common that differ from the langurs south of the Brahmaputra. The Jia-Bhoreli (known as Kameng in Arunachal Pradesh) is an effective barrier separating the two subspecies only in its middle to lower reaches. It is not an effective barrier in its upper reaches. There, besides showing seasonal variation, the pelage is variable even within a group, and assigning any of the color patterns that characterize the subspecies is difficult. Even the dark *tenebricus* seems to be similar to the langurs of eastern Assam, south of the Brahmaputra, when they have their seasonally dark pelage. The pattern of the cap of *brahma* and some differences in pelage color, however, still separate them from *tenebricus*. The shape of the cap of *brahma* is more akin to *T. p. pileatus* to the south of the Brahmaputra.

Regarding the capped langurs separated by the Brahmaputra River (Choudhury 1989a, 2013), field observations and a review of several hundred photographs have indicated features that distinguish them. The most distinct characteristic is the cap and its contact with the ears. In capped langurs to the south of the Brahmaputra, the gray cap is separate, forming an “army-cut hairstyle”: *pileatus* (Fig 3; Photos 4a and 5a). In capped langurs to the north of the river, the darker gray cap extends to the ear: *tenebricus* (Fig. 3; Photos 4b and 5b), *brahma* (Fig. 3; Photos 4c and 5c). The side-whiskers of *tenebricus* and *brahma* are notably longer than those of *pileatus* (Fig 3). The key feature distinguishing *tenebricus* from *brahma* is the cap (Fig. 3). In *tenebricus* it is shaggy, with hairs radiating away from the forehead. In *brahma* the cap is less shaggy and more of a pom-pom similar to that of *pileatus*, but with the gray cap extending down to the ears (not in *pileatus*) (Fig. 3). See Table 2, Figure 3, and photos 1–10 for other distinguishing features.

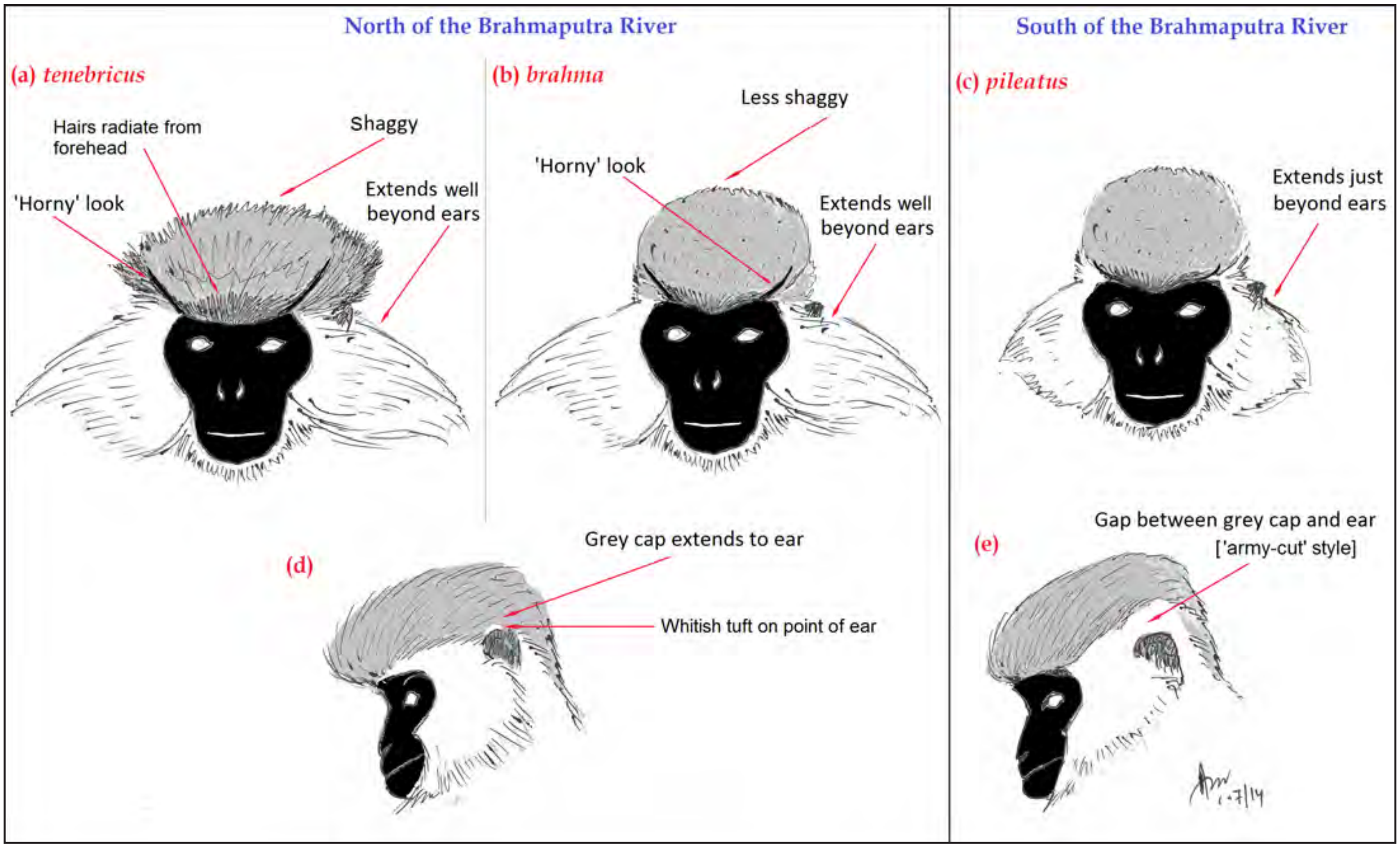


**Figure 3.** Variation between capped langurs north (left and center) and south (right) of the Brahmaputra River. Drawings based on individuals observed in Manas (a); Harmoty, Lakhimpur (b); Kaziranga (c and e); and Potasali, Balipara Reserved Forest, outside Nameri (d). See also the photographs. Illustrations by Anwaruddin Choudhury.

## Discussion

Digital cameras and careful observation facilitate a more discerning identification of consistencies in subspecific variation in capped langurs. The seasonal variation in pelage is so significant that photos of the same group of langurs (Photos 1a, 1b and 2a, 2b) or langurs from the same locality (Photos 3a, 3b, 3c) could well be described as two distinct races if based on a few specimens deposited in a museum. Even in the same group at the same time of year colors can be markedly different, darker or lighter gray backs for example, in different individuals. After more than three decades observing this species in the wild, I have been able to identify differences that consistently apply to each of the subspecies. The cap and its extent vis-à-vis the ears is the most noteworthy, separating capped langurs north and south of the Brahmaputra. To the north of the river, the langurs are separated in Assam by the Jia-Bhoreli River, and in Arunachal Pradesh, where it is known as the Kameng River, they are separated as far as the middle reaches. In the higher elevations of the Himalaya, the river is narrower and there is no barrier. Visitors to Nameri National Park see both *tenebricus* and *brahma* and there is a likelihood of confusion. The main part of the park is to the east of the Jia-Bhoreli River where *brahma* occurs, while *tenebricus* occurs in the tourist facilities at Potasali, outside the park boundary (in Balipara reserved forest) to the west of the river.

There is no zoogeographic barrier separating the nominate race and *durga* Wroughton, 1916. The elevational differences used to justify the separation of the two forms are insignificant—*pileatus* believed to occupy higher elevations (above 600 m) and *durga* lower elevations (below 600 m) (Groves 2001). The specimens of *pileatus* from near Tura, Garo Hills, were from about 420 m above sea level (Hinton 1923), while *durga* has been observed above 1,000 m in Mizoram and central Assam. Langurs from higher elevations have a seasonally brighter color, like *durga*, and *durga* also shows seasonal changes to a lighter color. The cap patterns, including the "army-cut" style, are also similar. In a single group or in adjacent groups, there can be individuals resembling *durga* and *pileatus* (Photos 3a, 3b, 3c). Hence, these I consider to belong to a single subspecies.

Capped langurs in the Mishmi Hills to the north of the Lohit River, and at very high elevations, for example, above 2,500 m in Nagaland (Saramati area) and eastern Arunachal Pradesh (Dapha Dum), may need further observation/examination to assign them to one or other of the subspecies. Similarly, those occurring at high elevations in the Great Himalaya in northernmost Arunachal Pradesh need to be studied further. The high elevation langurs have thicker fur and are slightly paler, but photos year round are required to reach any conclusion regarding their affinity.

It is unlikely that all individuals in a population change their coat color at the same time, and there is also the transitional period to be considered, as well variation between individuals, and differences in sex and age. On December 2, 1992, in Borajan Reserved Forest (now part of the Bherjan–Borajan–Podumoni Sanctuary), Tinsukia district in eastern Assam, I was able to observe two adult male *pileatus* (form *durga*). On one the whiskers and upper ventrum were orange, like *durga*, while in the other the whiskers and ventrum were pale yellow, like *pileatus*. On October 6, 1992, one of the males looked like a *tenebricus* (except in its cap pattern) with a deep gray dorsum and yellowish-orange ventrum. On June 12, 1993, one of the males had a similar dark coloration, but an adult female had a gray (not dark) dorsum. On November 1, 1991, in the Dhansiri reserved forest, Karbi Anglong district, I observed two adult females both with a pale gray dorsum, but one had a creamy with reddish-tinged ventrum and the other (with an infant) had a deep orange-yellow ventrum.

The original descriptions of the subspecies were based on the pelage color of the specimens when they were collected. There was no mention of individual or seasonal variation. Pocock (1928), however, did write that "the colour, however, varies in different individuals assigned to this race." Hinton's (1923) descriptions were in greater detail than those of Wroughton (1916). Pocock (1928) erroneously said that the form *durga* also occurs north of the Brahmaputra on the assumption that there was specimen from Lakhimpur (from where *brahma* was also taken). However, Lakhimpur at that time extended north and south of the Brahmaputra. While the specimens of *brahma* were from the north of the river, those of *durga* (obtained as *saturatus* Hinton, 1923, from Bor Hapjan, now in Tinsukia district) were from the south of the river.

The distinguishing features of the *T. pileatus* forms, especially the facial hair patterns (Table 2), clearly and consistently distinguish *T. pileatus* north of the Brahmaputra River (*tenebricus* and *brahma*) from those to the south (the nominate subspecies *pileatus*). To the north of the Brahmaputra, this is also true for *tenebricus* and *brahma* along the lower reaches of the Jia-Bhoreli River, but forms intermediate between them appear as the river narrows in the upper reaches. The consistent differences between the three forms indicate the possibility of classifying them as distinct species following the Phylogenetic Species Concept, as espoused by Groves (2001, 2004, 2012). However, I continue to treat them as subspecies rather than full species. The three populations identified are segregated completely by one very large river and incompletely by one large river, and I see them clearly as diverging lineages, best characterized as races of a single species. This arrangement follows the subspecies designations of other populations of large mammals in the region, including, for example, tigers, leopards, and wolves.

The survival of the capped langur, and other forest-dwelling animals, is threatened by habitat destruction through logging, encroachment, *jhum* or slash-and-burn shifting cultivation (of the hill tribes), and monoculture forest plantations. Such destruction of the forest is not only resulting in a decrease in habitat and a decline in numbers of langurs, but also creating fragmentation. Hunting for its meat is a serious threat in some parts of Assam, central and eastern Arunachal Pradesh, parts of Meghalaya and Tripura, hill districts of Manipur, and throughout Nagaland and Mizoram. The Nyishis of Arunachal Pradesh also hunt it to use its pelt to make traditional *dao*-sheaths. Unsustainable harvesting of bamboo for large paper mills (for example, at Jagiroad, Panchgram and Jogighopa in Assam, and Tuli in Nagaland), petroleum mining and exploration (eastern Assam and adjacent areas of Arunachal Pradesh), and open-cast coal and limestone mining (in parts of Meghalaya and eastern Assam) are some of the other conservation issues; they not only destroy the habitat, but also cause pollution and disturbance.

*Trachypithecus pileatus* is protected under Schedule I of the Wild Life (Protection) Act of India, the highest conservation status in the country. Enforcement in the field, however, is virtually non-existent except in some protected areas. Most local communities are unaware of its legal status. *Trachypithecus pileatus* occurs in at least 53 notified protected areas in Northeast India (Table 1).

Although the capped langur is still widely distributed throughout Northeast India, there are many small, isolated populations as a result of the rapid fragmentation of their forests. Many of these populations are not viable in the mid- to long term, and it is only a matter of time that the species will become locally extinct in pockets such as Mijikajan tea estate (Sonitpur district), Hatipoti village (Tinsukia district), Diroi and Sola reserved forests (both in Sivasagar district). It has already been extirpated in many areas; for example, Manipur valley, many parts of Nagaland and Mizoram except in some isolated pockets, the plains of Lakhimpur district, most of the tableland of the Meghalaya plateau, and many parts of Sonitpur district in Assam. The entire population of langurs and also other primates have vanished from the 900-km² rain forest tract comprising the Nambor (south block), Diphu, and Rengma reserved forests in Golaghat district (Assam) because of the border problems with Nagaland and subsequent felling, poaching and encroachment (Choudhury 1999). The last stray langurs were reported there in the 1980s.

What could be the estimated number of capped langurs? An exercise was carried out in Assam in the 1980s estimating the number of groups present, and multiplying them by mean group size. The figure for Assam came to 39,000 (Choudhury 1989a). No population estimate was available for other states of Northeast India, but none were likely to have higher numbers than Assam at that time. The presence of groups was ascertained through direct observation and from local forest staff and people from fringe villages.

A similar exercise between 2008 and 2014 in the same areas of Assam, using a mean group size of 9.97 (range: 5–14; n= 33; Choudhury 2012) indicated 18,600 (range: 17,500–20,000) langurs, reflecting well the extent of habitat loss. A similar exercise was not possible for the entire northeast, but in view of the larger area of available habitat, much of it in relatively inaccessible areas, the state of Arunachal Pradesh is currently likely to have a larger number than Assam.

Adequate protection of the existing national parks and sanctuaries, and the creation of more protected areas (such as Dhansiri and Lumding in Assam; Satoi and Saramati in Nagaland, Inner Line in Mizoram), enlargement (wherever possible) of existing protected areas, stricter enforcement of the wildlife law, provision of synthetic or cotton *dao*-sheaths (that could mimic a capped langur skin) for the Nyishi tribe of Arunachal Pradesh (they would find it acceptable as they told me during various contacts with them), and awareness programs will help ensure the survival of the capped langur.

## Conclusions

1. The Brahmaputra River clearly separates populations of the northern capped langurs (*tenebricus* and *brahma*) from the southern *pileatus* with its distinct "army-cut hairstyle" cap. Both *pileatus* and *durga* have this unique cap.
2. The subspecies *tenebricus* is distinct in having a cap/crown with radiating hairs.
3. Both *brahma* and *tenebricus* lack "army-cut hairstyle" caps. The cap of *tenebricus* differs from that of *brahma* in having radiating hairs.
4. The north bank langurs have longer cheek whiskers than their southern counterpart.
5. Pelage color has seasonal variations that may not occur at the same time over the range. The form *durga* (now synonymized with the nominate race) in Bangladesh and southern Assam may assume a deep orange-yellow ventrum earlier or later than those in Kaziranga and Tinsukia in eastern Assam.
6. The adults and immatures, and males and females show variations. In the same group, not all adults assume the bright ventral color at the same time.
7. Immatures are generally less bright and may have pale tail ends.
8. The facial hair patterns, including the cap, provide a more clear-cut segregation of the subspecies than the variable and confusing pelage colors.
9. The number of capped langurs is declining.

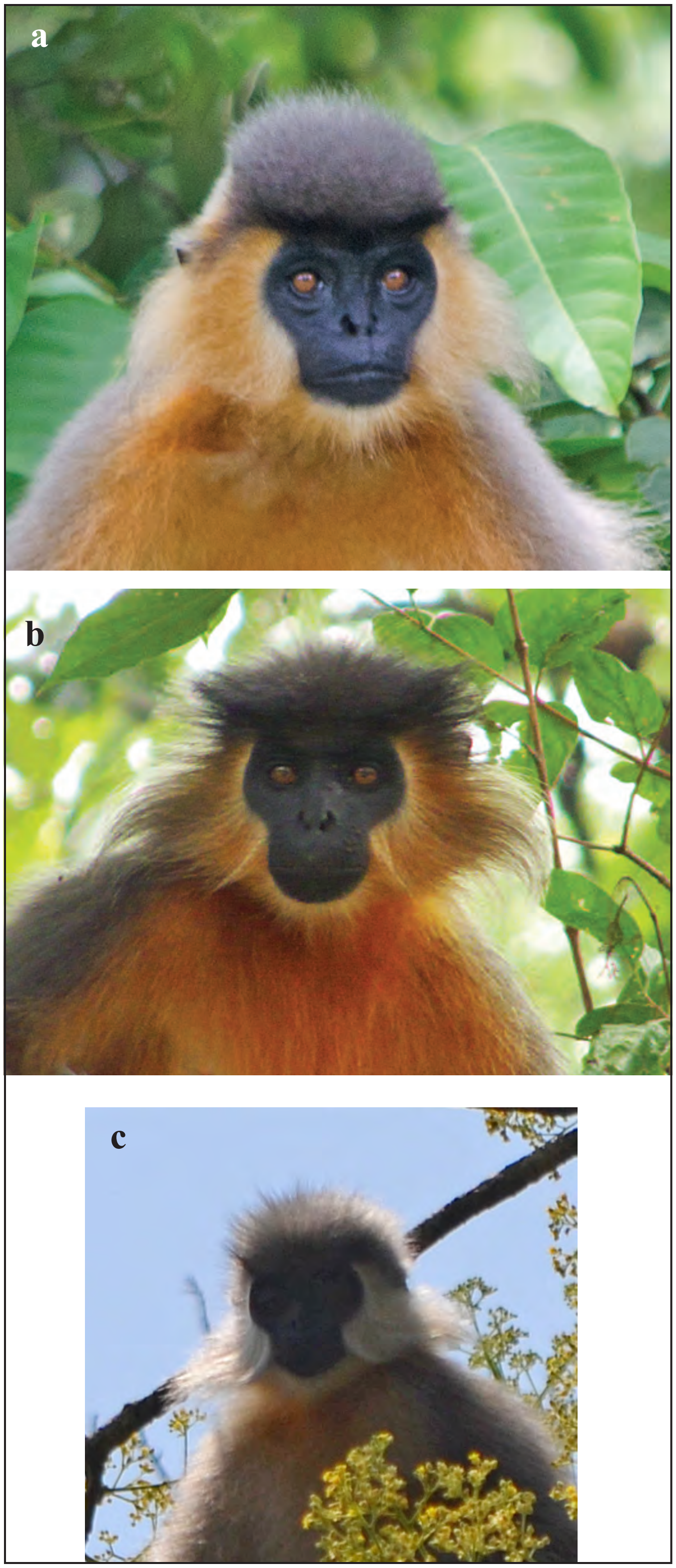
## Acknowledgments

I am most grateful to a large number of forest officials for their assistance during this long study. Valuable discussions and sharing of knowledge at different times in the past with acclaimed authorities such as Colin P. Groves and George Schaller are gratefully acknowledged. I also thank bureaucrats, villagers, local guides and family members for their help and encouragement. Thanks are also due to Arup Ballav Goswami, Anirban Datta Roy/Samrakshan Trust, Udayan Borthakur and Khairuzzaman Mazumdar for kindly allowing me to use their photographs.

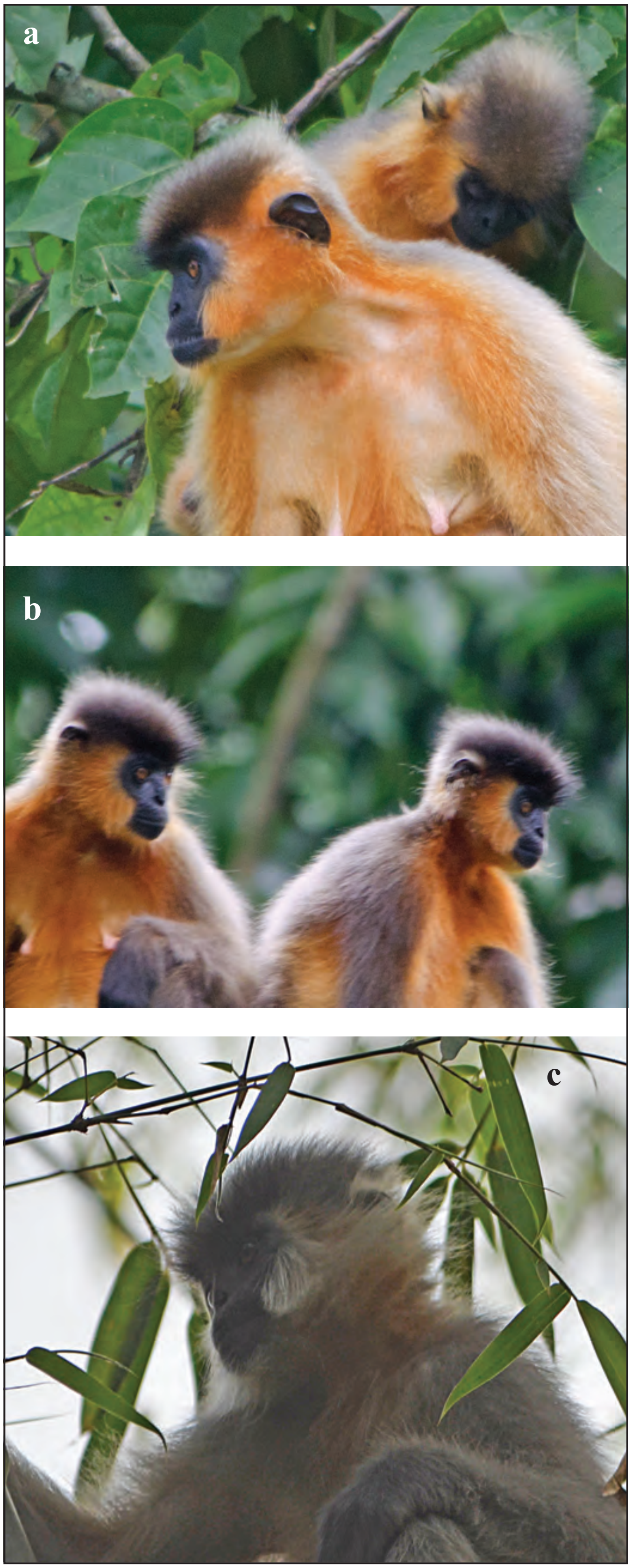
**Photos 1.** Pelage color. Seasonal color variation makes pelage color redundant for the segregation of subspecies. (a) *T. p. tenebricus* from Manas Tiger Reserve, north of the Brahmaputra River and west of the Jia-Bhoreli River, 15 November. (b) *T. p. tenebricus* from Manas Tiger Reserve, 22 February. Photos by Anwaruddin Choudhury.

**Photos 2.** Pelage color. Variation in color among individuals on the same day in the same group makes pelage color redundant for the segregation of subspecies. (a) *T. p. pileatus* from Hollongapar Gibbon Sanctuary, south of the Brahmaputra River, in May showing deep orange venter. (b) *T. p. pileatus* from the same group in Hollongapar Gibbon Sanctuary in May showing light orange venter. Photos by Arup Ballav Goswami.

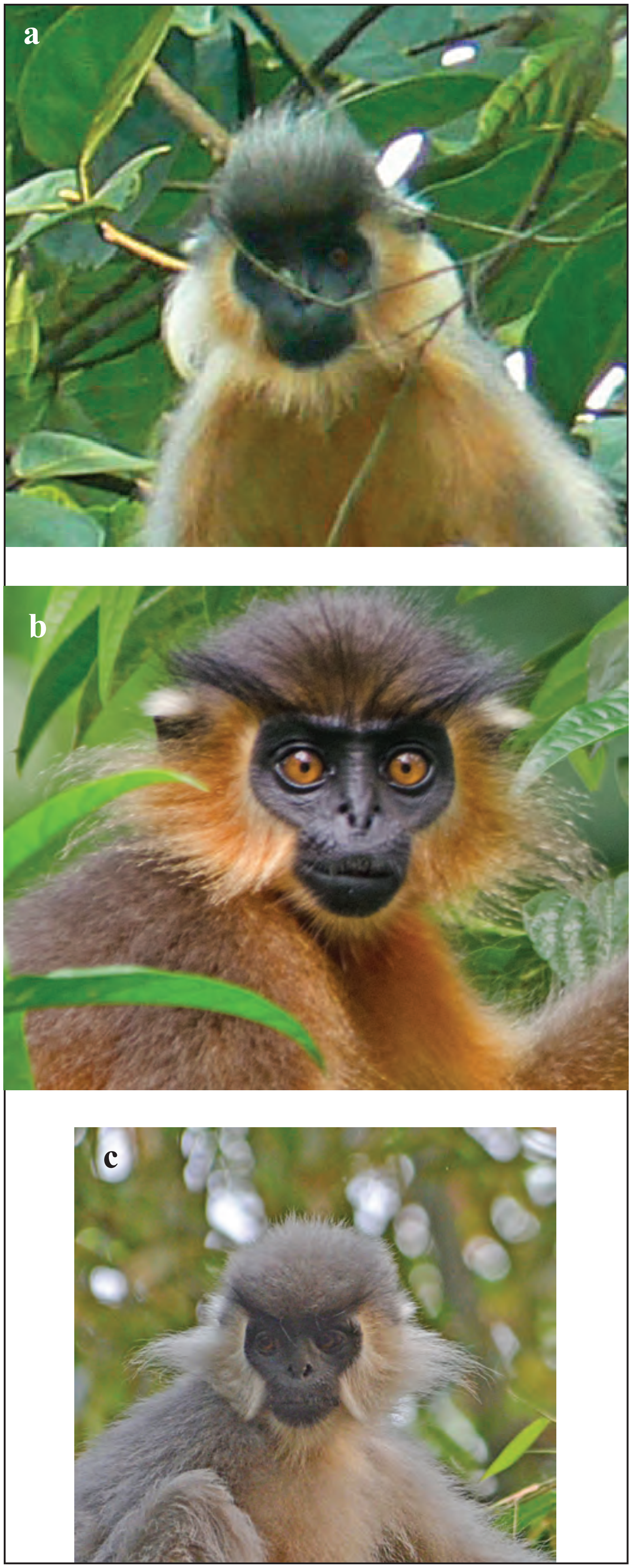
**Photos 3.** Pelage color. Color variation in a single locality showing how pelage color as a character can confuse attempts to distinguish subspecies. These photos show why the forms *pileatus* and *durga* should be considered synonyms. (a) *T. p. pileatus* (form *durga*) from Rosekandy, Cachar district, Assam, showing an unusually deep orange even on the arms and thighs, 4 June. (b) *T. p. pileatus* (form *durga*) from Rosekandy, Cachar district, Assam, showing orange whiskers and ventrum and grey arms and thighs, 4 June. (c) *T. p. pileatus* (form *durga*) from Rosekandy, Cachar district, Assam, showing a lack of any orange or reddish but uniform creamy or light yellowish whiskers and ventrum, resembling the description of the nominate form *pileatus*, 22 May. Photos by Khairuzzaman Mazumdar.



**Photos 4.** Frontal view. Note the cap, length of the side whiskers in relation to the ears, the contact zone of the cap and forehead, and the sides of the cap (giving an appearance of horns). (a) *T. p. pileatus* male from Kaziranga National Park, south of the Brahmaputra River, 21 July. (b) *T. p. tenebricus* male from Manas National Park, north of the Brahmaputra River and west of the Jia-Bhoreli River , 15 November. (c) *T. p. brahma* male from Behali Reserved Forest, north of the Brahmaputra River and east of the Jia-Bhoreli River, 1 April. Photos by Anwaruddin Choudhury.



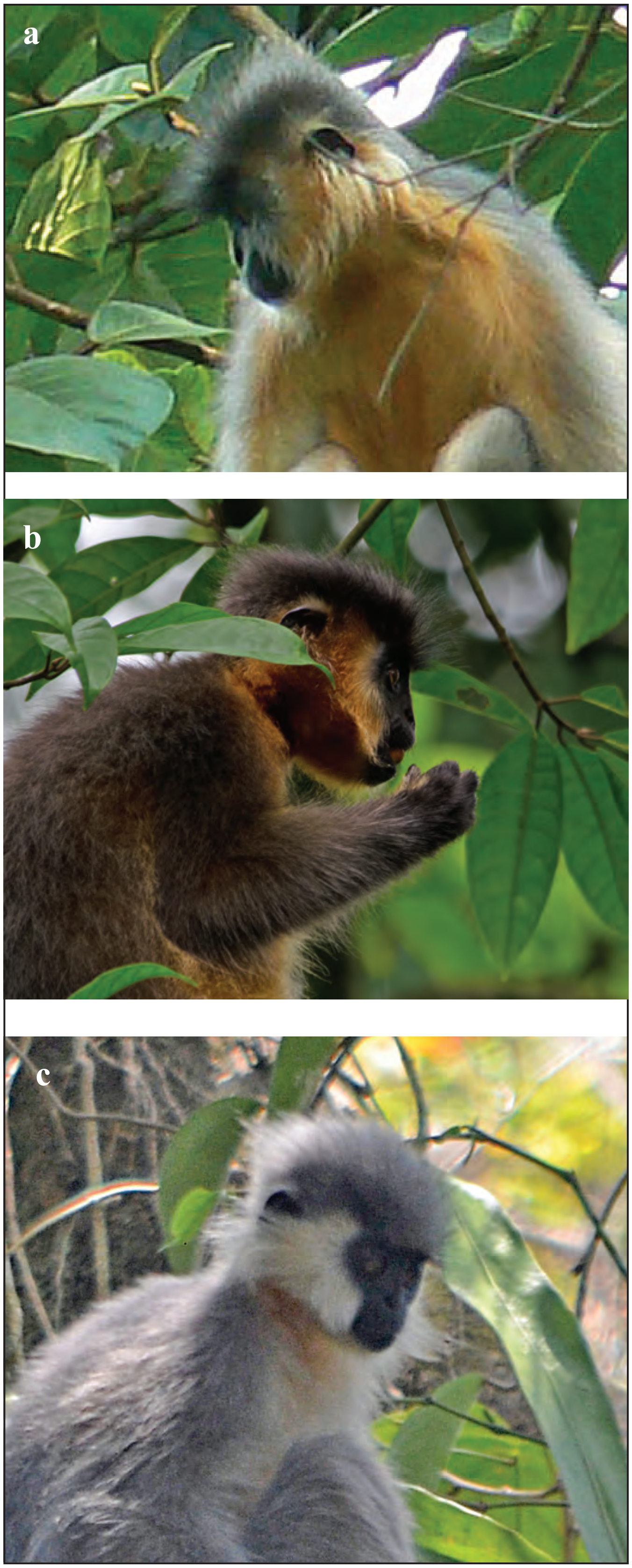
**Photos 5.** Side view: Note the cap in relation to the ear. (a) *T. p. pileatus* from Kaziranga National Park, south of the Brahmaputra River showing the 'army-cut' hair-style of the cap. (b) *T. p. tenebricus* from Balipara Reserved Forest, north of the Brahmaputra River and west of the Jia-Bhoreli River. The location is near but outside Nameri National Park and is separated from it by the Jia-Bhoreli River. (c) *T. p. brahma* from Harmoty, Lakhimpur, north of the Brahmaputra and east of Jia-Bhoreli River. Photos by Anwaruddin Choudhury.



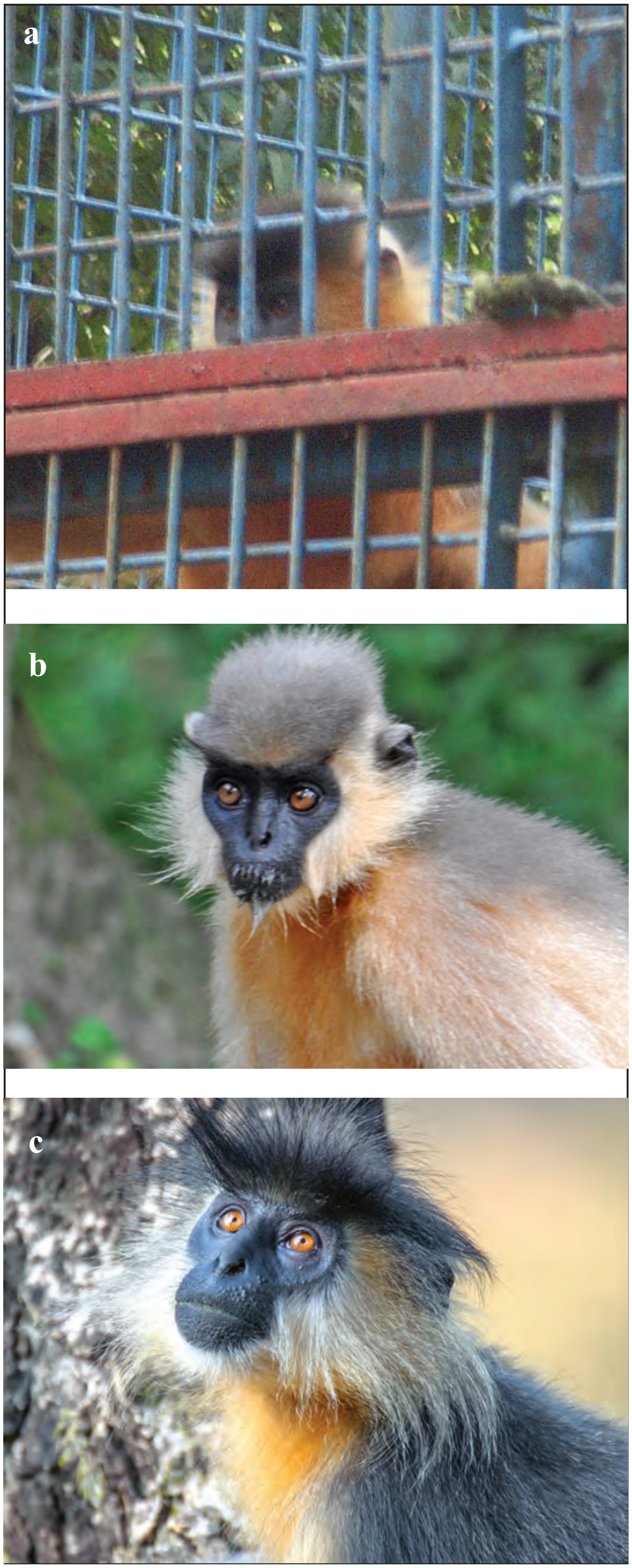
**Photos 6.** Frontal, general views. (a) *T. p. pileatus* from Baghmara Reserved Forest, Garo Hills, south of the Brahmaputra, 30 May. Photo by Anirban Datta Roy/ Samrakshan. (b) *T. p. tenebricus* from Balipara Reserved Forest, north of the Brahmaputra River and west of the Jia-Bhoreli River, 21 July. Photo by Anwaruddin Choudhury. (c) *T. p. brahma* from Harmoty, Lakhimpur, north of the Brahmaputra River and east of the Jia-Bhoreli River, 8 April. Photo by Anwaruddin Choudhury.

**Photos 7.** Frontal, general views. (a) *T. p. pileatus* from Inner Line Reserved Forest, Hailakandi, south of the Brahmaputra, March. (b) *T. p. tenebricus* from Deothang, Bhutan, north of the Brahmaputra River and west of the Jia-Bhoreli River, 30 May. (c) *T. p. brahma* from Mijikajan, Sonitpur, north of the Brahmaputra River and east of the Jia-Bhoreli River, September. Photos by Anwaruddin Choudhury.

**Photos 8.** Frontal, general views. (a) *T. p. pileatus* from Dhansiri Reserved Forest, Karbi Anglong, south of the Brahmaputra River, December-January. (b) *T. p. tenebricus* from Sessa Orchid Sanctuary, Arunachal Pradesh, north of the Brahmaputra River and west of the Jia-Bhoreli River, May. (c) *T. p. brahma* from Behali Reserved Forest, Sonitpur, north of the Brahmaputra River and east of the Jia-Bhoreli River, 1 April. Photos by Anwaruddin Choudhury.



**Photos 9.** More side views. (a) *T. p. pileatus* from Baghmara Reserved Forest, Garo Hills, south of the Brahmaputra River. Photo by Anirban Datta Roy/ Samrakshan. (b) *T. p. tenebricus* from Balipara Reserved Forest, north of the Brahmaputra River and west of the Jia-Bhoreli River. Photo by Anwaruddin Choudhury. (c) *T. p. brahma* from Behali Reserved Forest, Sonitpur, north of the Brahmaputra River and east of the Jia-Bhoreli River. Photo by Anwaruddin Choudhury.



**Photos 10.** More side views. (a) *T. p. pileatus* in Dhaka zoo, Bangladesh, south of the Brahmaputra River. Photo by Anwaruddin Choudhury. (b) *T. p. pileatus* from Hollongapar Gibbon Sanctuary in May. Photo by Arup Ballav Goswami. (c) *T. p. tenebricus* from Manas National Park, north of the Brahmaputra River and west of the Jia-Bhoreli River. Photo by Udayan Borthakur.

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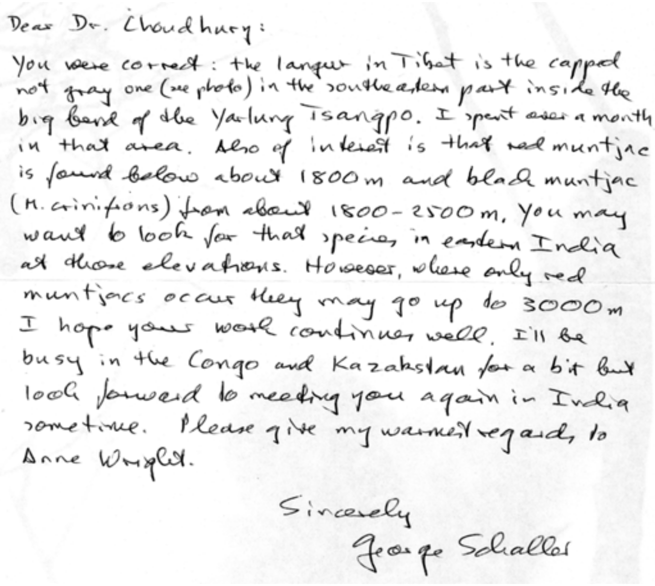
**Appendix.** Letter from Dr. George B. Schaller concerning capped langurs. Dated: 2000–2001



Dear Dr. Choudhury:

You were correct: the langur in Tibet is the capped not gray one (see photo) in the southeastern part inside the big bend of the Yarlung Tsangpo. I spent over a month in that area. Also of interest is that red muntjac is found below about 1800m and black muntjac (M. crinifrons) from about 1800-2500m. You may want to look for that species in eastern India at those elevations. However, where only red muntjacs occur they may go up to 3000m I hope your work continues well. I'll be busy in the Congo and Kazakstan for a bit but look forward to meeting you again in India sometime. Please give my warmest regards to Anne Wright.

Sincerely
George Schaller

*Primate Conservation* 2014 (28): 159−163

# Population Status of Phayre's Langur *Trachypithecus phayrei* in Sepahijala Wildlife Sanctuary, Tripura, Northeast India

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**Abstract:** We studied the population status of Phayre's langur (*Trachypithecus phayrei*) in the Sepahijala Wildlife Sanctuary (23°37'N to 23°42'N and 91°17'E to 91°21'E), West Tripura district, Northeast India, from December 2009 to February 2010. Using line transect and recce sampling, we recorded seven groups comprising 95 individuals. The average group size was estimated at 13.14 individuals per group (range 8–19, SD = 3.77). The population comprises 7.4% adult males, 34.7% adult females, 23.2% of sub adults, 26.3% juveniles, and 8.4% infants.

**Key Words:** Phayre's langur, population status, Sepahijala Wildlife Sanctuary, threats, Tripura.

## Introduction

Phayre's langur, *Trachypithecus phayrei* (Blyth, 1847), is found in Bangladesh, Myanmar, China, India, Thailand, and Vietnam (Roonwal and Mohnot 1977; Stanford 1988; Gupta and Kumar 1994; Srivastava 1999; Bose 2003; Min *et al.* 2005). In India, the nominate subspecies is found only in the lower northeastern states bordering Bangladesh (Menon 2003); Tripura, Mizoram, and Assam, from sea level to 800 m (Mukherjee 1982; Choudhury 1987, 1994a, 1994b; Srivastava 1999; Bose 2003; Aziz and Feeroz 2009). It inhabits subtropical evergreen, broadleaf, deciduous, and bamboo forests and semi-evergreen forests (Srivastava and Mohnot 2001; Molur *et al.* 2003; Walker and Molur 2007). Phayre's langur is found in higher densities in mixed-species plantations than in monoculture plantations (Gupta 1997). In Tripura, Phayre's langurs are reported from all over the state, but more in the southern districts than in the western and northern districts (Mukherjee 1982; Gupta 1997). The healthiest population is found in the Trishna Wildlife sanctuary (Gupta 2001). The species has been studied by Mukherjee (1982), Gupta and Kumar (1994) and Gupta (1997, 2001). Gupta (2001) recorded 81 plant species in the diet of a Phayre's langur group in the Sepahijala Wildlife Sanctuary. He listed the major food plants and described the group composition and the breeding season. There have been no studies carried out on Phayre's langur in the Sepahijala Wildlife Sanctuary since 1993. In this paper, we report on the population status and threats to Phayre's langur in the Sepahijala Wildlife Sanctuary.

## Study Area

The Sepahijala Wildlife Sanctuary (1,853 ha) is situated in the western part of Tripura, in the Bishalgarh Civil Subdivision of West Tripura district, about 20 km from the capital Agartala (Fig. 1). It lies between 23°37'N and 23°42'N and 91°17'E and 91°21'E, altitude 50 m above sea level. It was created in 1987 with an area of 18.53 km² but, in 2008, 5.08 km² of the Sepahijala Wildlife Sanctuary was declared a Clouded Leopard Sanctuary to protect the endangered clouded leopard (*Neofelis nebulosa*) (Chakraborty 2004–2005). Sepahijala Zoological Park was established in the buffer zone of the Sepahijala Wildlife Sanctuary with the approval of Central Zoo Authority (CZA). The terrain is undulating, with small hillocks. Summer temperatures vary from 20.5°C to 36.2°C, and winter temperatures from 7°C to 27.1°C. Annual rainfall is about 234 cm.

The forest is classified as Moist Mixed Deciduous, with Secondary Moist Bamboo Brakes. There are also man-made forests of sal (*Shorea robusta*), teak (*Tectona grandis*), patches of acacia or wattle (*Acacia auriculiformis*) and rubber (*Hevea*). The five primates found in Sepahijala Wildlife Sanctuary are Phayre's langur (*Trachypithecus phayrei*), capped langur (*Trachypithecus pileatus*), pig-tailed macaque (*Macaca nemestrina*), Rhesus macaque (*Macaca mulatta*) and the Bengal slow loris (*Nycticebus bengalensis*).

Habitat degradation caused by eco-tourism and the communities living in and around the sanctuary are the main threats to the sanctuary's integrity. Tourism is associated with rubbish (plastics). Teasing the monkeys and playing loud music inside the sanctuary is also an issue. There is a road inside the sanctuary used for tourism, resulting in occasional road kill.

## Methods

### *Population studies*

A preliminary survey was carried out to record the habitat types and habitat quality, and to become familiar with the trails that would be used for the survey. Previous census data of the Phayre's langur was obtained from the forest department, and local people were questioned about how many Phayre's langur groups they believed occurred in the sanctuary.

From December 2009 to February 2010, we carried out surveys using line transect and recce sampling on all trails in the sanctuary (Swapna *et al.* 2008). Transects were walked from 05:30 to 12:00 and from 14:00 to 18:00 or sunset. On each survey we stopped every 200 m to look and listen for monkeys. When a group was seen, we recorded its size and age-sex composition. Only total group counts were used to estimate the group size (Srivastava, *et al.* 2001a, 2001b; Fashing 2002; Pruetz and Leasor 2002; Srivastava 2006; Medhi *et al.* 2007). We recorded the time they were seen, GPS location, duration of observation, and the tree species they were in or feeding on. Each trail was surveyed three times.

Individuals were classified as adult male (AM), adult female (AF), subadult (SA), juvenile (J) or infant (I) based on the morphological characters and differences described by Bhattacharya and Chakraborthy (1990), Choudhury (1987), Srivastava (1999) and Gupta (2001). Some subadults could not be sexed due to the dense vegetation and poor visibility.

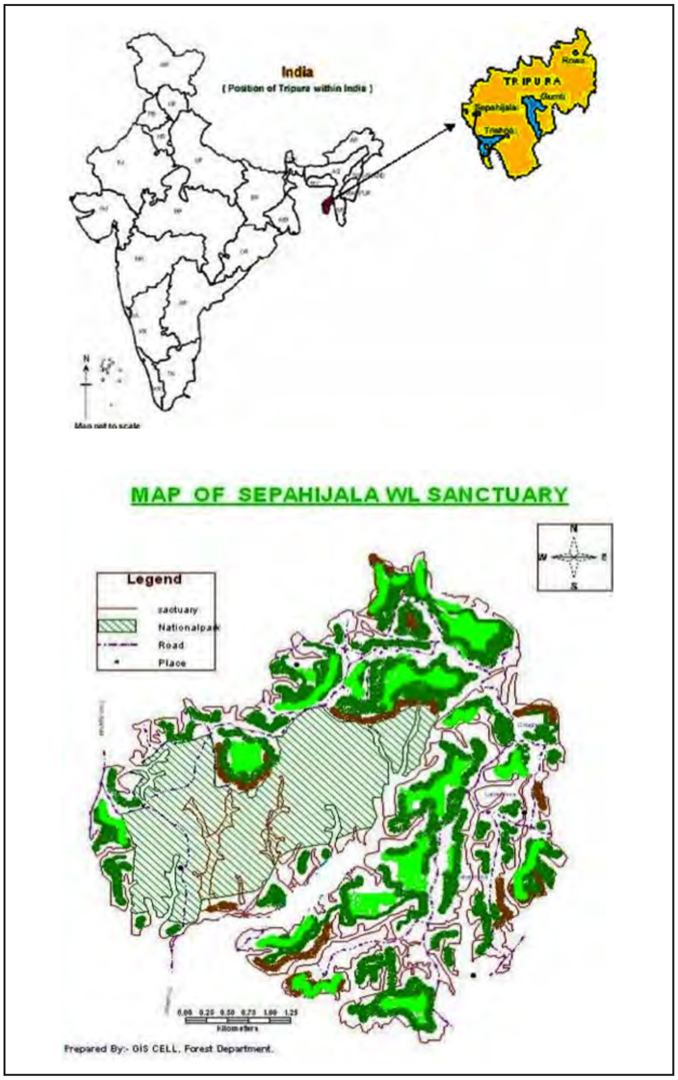

**Figure 1.** The Sepahijala Wildlife Sanctuary, Tripura, India.

**Table 1.** Survey trails and their vegetation types in the Sepahijala Wildlife Sanctuary, West Tripura.

| | Length (km) | Habitat |
|---|---|---|
| 1 | 1.4 | Agricultural land one side, the other side a young sal plantation, young sal plantation, mature sal plantation with bamboo brake, mixed bamboo patch, *Cassia* plantation |
| 2 | 2.1 | Open area, agricultural land and nurseries, open area with scrubby vegetation and scattered trees, human habitation, mature sal mixed forest, mature sal mixed forest with bamboo brakes, mixed bamboo mature forest – closed canopy, mature mixed forest, closed canopy, secondary mixed forest and rubber plantation |
| 3 | 1.95 | Secondary teak mixed forest, secondary teak mixed forest, secondary forest, mature mixed forest, mature mixed forest – closed canopy, rubber plantation |
| 4 | 3.6 | Sal mixed forest in a small *Acacia* plantation, sal mixed forest, teak mixed forest, open area – agricultural lands, open area – human habitation, bamboo dominated secondary mixed forest, secondary mixed forest, dense secondary mixed forest, bamboo-dominated secondary dense mixed forest |
| 5 | 3.35 | Mature sal forest, open area – agricultural land, secondary mixed forest, 10-ha agar plantation – agar mixed patch, open area – human habitation, secondary mixed forest, secondary bamboo dominated mixed forest (bamboo planted), dense mature mixed forest patch (small patch is close to the zoo, probably why it is less disturbed) |
| 6 | 3.25 | Dense mature mixed forest patch (small patch close to the zoo probably why it is less disturbed), secondary mixed forest, secondary mixed dense forest, open area – agricultural lands, secondary teak mixed forest (open), secondary teak mixed forest (open) with bamboo plantation nearby, open area – grass plantation area, bamboo dominated secondary mixed open forest and secondary sal mixed forest |
| 7 | 3.7 | Mixed partially dense forest with patches of acacia, mixed partially dense forest with teak plantation, open shrub jungle, open mixed forests with bamboo brakes, mixed forest with bamboo and open in nature, open area with pond surrounded by a mixed dense forest, open mixed forest shrubby, sal mixed forest with partially dense canopy cover, sal mixed forest with dense canopy cover, sal mixed forest open canopy, mixed forest with bamboo, secondary mixed forest open area, mixed forest young plants water body, mixed forest partially dense slope followed by open area, shrub jungle with teak |
| 8 | 2.0 | Open shrub, dense scrub forest, dense shrub jungle with occasional sal trees, open shrub with bamboo clumps, and bamboo plantation. |

In adults, sex was determined by the sex organs and by the pale yellow patch that surrounds the eyes. It is circular or elliptical in the males, and triangular or cone shaped in the females (Choudhury 1987; Gupta 2001). The pale patch is not prominent in juveniles and infants. The juveniles were identified based on their closer contact with their mothers when they rest and roost. The infants were identified by their orange color that begins to change to adult coloration at about three months of age (Srivastava 1999). Groups were monitored to record changes in size. Births typically occur from November to February (Gupta 2001).

### *Forest disturbance*

We recorded evidence of human activities in a 10-m radius at points every 200 m along the trails. Disturbance included wood cutting, grazing, logging, cultivation, houses, bamboo collection (illegal), firewood collection, forest fires, and trampling. The presence of dung indicated grazing pressure. The various forest types along each transect were also recorded (Table 1).

## Results

### *Preliminary survey*

The habitat types found in the sanctuary include moist mixed deciduous forest, sal (*Shorea robusta*) forest, sal (*Shorea robusta*) mixed forest, teak (*Tectona grandis*) mixed forest, secondary bamboo brakes, and bamboo plantations. The previous census data of Phayre's langur recorded four groups, comprising 46 individuals (Tripura Forest Department). Reports from local people indicated that the population was made up of just three troops.

### *Population*

An estimated seven groups, comprising 95 individuals, were recorded during the study period (Table 2). They were identifiable by their size and composition. Groups four and seven were the same size (12 individuals), but differentiated by the broken tail of the adult male in group 7. The smallest group had eight individuals and the largest group 19. The average group size was 13.14 individuals (range 8–19, SD = 3.77). Percentage group composition was 7.4% adult males, 34.7% adult females, 23.2% of subadults, 26.3% juveniles and 8.4% of infants. The groups were found to have one male and from three to seven females; a uni-male, multi-female social system. Eight births were recorded during the months of January and February. A single infant was present in each group except for one, which had two infants.

### *Threats*

Human disturbance in the forest included logging, grazing, cultivation, firewood collection, fires, illegal bamboo collection, trash (plastics), and tourists agitating and teasing the monkeys and other wild animals. The percentage recorded occurrence was as follows: grazing 20%, cutting of trees for timber 20%, cultivation 16%, human habitation 7%, illegal bamboo collection 2%, forest fires 2% and other illegal activities such as firewood collection 24% (Fig. 2). Grazing and firewood collection are the most frequent disturbances in the sanctuary. Timber collection was prominent on three of the trails. Transect number three that traversed the rubber plantation and passed through the mixed deciduous forest was the least disturbed, and five of the seven groups of the Phayre's langur groups were seen there. Since the Sepahijala Zoological Park is located by the wildlife sanctuary, a road connecting the zoological park with the highway that is used by tourists is also a threat to the Sepahijal Wildlife Sanctuary. During the study period we reported two road kills; a porcupine and a macaque.

## Discussion

The population of Phayre's langur in the Sepahijala Wildlife Sanctuary was estimated at seven troops comprising 95 individuals (eight of them infants). This is higher than that of

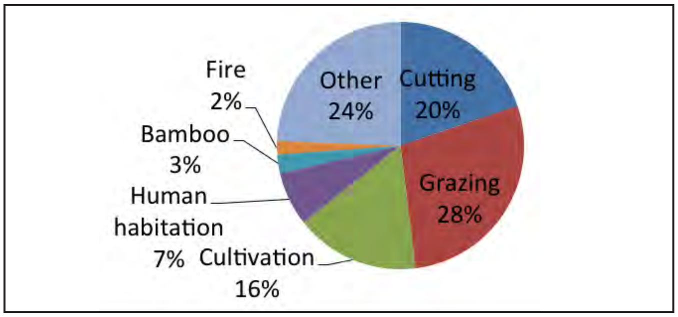

**Figure 2.** Disturbances recorded in the Sepahijala Wildlife Sanctuary

**Table 2.** Size and composition of the Phayre's langur (*Trachypithecus phayrei* phayrei) groups recorded in the Sepahijala Wildlife Sanctuary.

| Group | Coordinates | | Adult male | Adult female | Subadult | Juvenile | Infant | Total |
|---|---|---|---|---|---|---|---|---|
| 1 | 23°39'57.9"N | 91°18'29.6"E | 1 | 6 | 5 | 5 | 1 | 18 |
| 2 | 23°39'58.4"N | 91°18'28.8"E | 1 | 4 | 4 | 3 | 1 | 13 |
| 3 | 23°39'58.7"N | 91°18'24.8"E | 1 | 5 | 2 | 4 | 1 | 13 |
| 4 | 23°39'59.6"N | 91°18'23.9"E | 1 | 4 | 3 | 3 | 1 | 12 |
| 5 | 23°40'00.3"N | 91°18'22.6"E | 1 | 3 | 1 | 2 | 1 | 8 |
| 6 | 23°40'01.9"N | 91°18'22.0"E | 1 | 7 | 4 | 5 | 2 | 19 |
| 7 | 23°39'48.2"N | 91°18'19.6"E | 1 | 4 | 3 | 3 | 1 | 12 |
| Total | | | | | | | | 95 |

the forest department census report (2009), which recorded 45 individuals in four groups. In 1993, however, Gupta estimated the Phayre's langur population in the Sepahijala Wildlife Sanctuary to be 17 groups, with group sizes ranging from 8 to 22 individuals. The reasons for the decline of the population are unclear. No poaching or deaths were recorded during the study period. The decline might be due to inbreeding or disease, which need to be investigated in future long-term studies. Disturbance from logging, firewood collection, bamboo collection, road kill (accidents by vehicles) and other anthropogenic pressures may also be indirect causes for the population decline. The Sepahijala Wildlife Sanctuary is a small but important protected area for Phayre's langur, and ecological studies and long-term monitoring of the population are needed.

## Acknowledgments

Doki Adimallaiah particularly thanks the Forest Department, Government of Tripura, for providing permission to carry out this study. We are also thankful to Mr. Nirod Baran Debnath, Wildlife Warden, Mr. Gautam Karmakar, Forest Ranger and Assistant Wildlife Warden, Mr. Biswajit Datta, and Mr. Lari Mohan Tripura, foresters of the Sepahijala Wildlife Sanctuary, for their kindness and support during the field work. Our gratitude goes to Mr. Maranko, Wildlife Crime Control Bureau, for his support in many ways. Special thanks also to N. Swapna and R. Deepak for their help during the study.

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# Distribution and Relative Abundance of the Slender Loris *Loris lydekkerianus* in Southern Kerala, India

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**Abstract:** Two subspecies of slender loris, the Mysore slender loris, *Loris lydekkerianus lydekkerianus*, and the Malabar slender loris, *Loris lydekkerianus malabaricus*, are known from Peninsular India. Their distributions overlap along the southern ridges of the Western Ghats. Although the distribution and abundance of the species is known for part of the state of Kerala, the full extent of the range of the species remains unclear. We surveyed forested areas of southern Kerala for a more comprehensive understanding of their distribution pattern and relative abundance. The range of *L. l. malabaricus* is confined to the western slopes of the Western Ghats. The Ariankavu pass and Palghat gap have created a barrier over a period of time, which has resulted in separate populations of *L. l. malabaricus*. As such, *L. l. malabaricus* is divided into three populations in Kerala—(1) Neyyar Wildlife Sanctuary in the southern tip to the south of the Ariankavu pass, (2) north of Ariankavu pass north to the Palghat Gap, and (3) north of the Palghat gap to the Aralam Wildlife Sanctuary. The relative abundance of *L. l. malabaricus* in most of the forest divisions of Kerala is <0.2 lorises/km, except in the Aralam Wildlife Sanctuary, Konni, Thiruvanthapuram, Nemmara, and Chimmoney.

**Key words**: Mysore slender loris, *Loris lydekkerianus lydekkerianus*, Malabar slender loris, *Loris lydekkerianus malabaricus*, Eastern Ghats, Western Ghats, Kerala, India

## Introduction

The slender loris, *Loris lydekkerianus* Cabrera, 1908, is one of the two nocturnal primate species found in India[1]. The two subspecies currently recognized are the Mysore slender loris, *Loris lydekkerianus lydekkerianus* and the Malabar slender loris, *Loris lydekkerianus malabaricus* Wroughton, 1917, inhabiting the dry forests of the Eastern and Western Ghats, and the wet forests of the Western Ghats, respectively. Although the distribution and abundance of the species is known for the state of Karnataka and some parts of Tamil Nadu, Kerala and Andhra Pradesh (Singh *et al.* 1999, 2000; Kumara *et al.* 2006; Radhakrishna *et al.* 2011), the entire range of the species in southern India remains unknown.

Based on the collection localities of museum specimens, it is evident that historically the River Tapti limited the species' range on the west coast, and the River Godavari on the east coast. The southeastern and southwestern limits of the distribution of lorises are still unclear and an understanding of the distribution pattern is problematic because of the complex geomorphology of southern India. The discontinuous Eastern Ghats, geographical barriers in the Western Ghats such as the Palghat Gap, and other discontinuities that form barriers such as plateaus and escarpments, in addition to historical land-use practices, have led to the fragmented wildernesses in South India (Radhakrishna *et al.* 2011). The dry forest subspecies is thought to be more abundant in the Eastern Ghats and eastern fringes of the Western Ghats, but the full extent of its range and its conservation status along the Western Ghats is not clear. The distributions of both the subspecies are said to overlap, which has never been really explored. As the wet forest subspecies occurs in lower densities in the Western Ghats, understanding its distribution and the quality of the remaining forests will help in prioritizing the forest patches for conservation. Radhakrishna *et al.* (2011) reported on the status and distribution of the slender loris in the northern and central parts of the state of Kerala. Here, I report on the results of surveys in southern Kerala, which complement the findings

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[1] The other is the Bengal slow loris, *Nycticebus bengalensis*.

of Radhakrishna *et al.* (2011), providing a picture of the overall pattern of distribution and abundance of the slender loris throughout the state.

## Methods

### *Survey sites*

We surveyed forests in southern Kerala from 77°08' to 77°24'E and 08°29’ to 09°48'N. They included the Periyar Tiger Reserve, three wildlife sanctuaries (Shendurney, Peppara and Neyyar) and seven reserve forests (Kottayam, Ranni, Konni, Achenkovil, Punalur, Thenmala, and Thiruvananthapuram) (Table 1, Fig. 1). The major vegetation types of southern Kerala are evergreen forests (on the western slopes of Western Ghats), semi-evergreen forests and degraded evergreen or semi-evergreen forests, and deciduous forests in some of the regions that are contiguous with the rain shadow areas of Western Ghats.

### *Data collection and analysis*

All the major forest patches in each forest range of the division were surveyed. Forest Divisions are the administrative units, which include administrative ranges known as Forest Ranges. Forest ranges were considered as the minimum sampling unit for a better understanding of the status of the species; a scheme which is also helpful in informing the local managers. The forest divisions include reserve forests, wildlife sanctuaries and a tiger reserve. Survey sites were selected based on the extent of forest cover in each forest range of the forest division. Night surveys were conducted between 2000 h and 0400 h on pre-determined transects that were already existing trails (as advised by Sterling and Ramaroson 1996, and Walsh and White 1999). Whether we used a vehicle survey or foot transect depended on access and the topography of the terrain (Singh *et al.* 1999, 2000; Nekaris and Jayawardene 2004). Vehicle speed was maintained at an average of 5 km/h (Singh *et al.* 1999). Walking speed averaged 1 km/h (Sterling and Ramaroson 1996). We used flashlights and headlamps; the eyes of slender lorises have a typical orange-red shine that can be seen from a distance of over 100 m (Singh *et al.* 1999, 2000).

The relative abundance index was calculated as the number of animals observed per kilometer (Sterling and Ramaroson 1996), with standard deviation. The number of

**Table 1.**Sampling effort, number of sightings, and encounter rate of slender loris, *Loris lydekkerianus lydekkerianus* and *L. l. malabaricus*, in different forest divisions of Southern Kerala (SD for sightings per kilometer is provided only if the sample size is more than two for each forest range.)

| Forest division | Forest range | Official status | Km walked/ motored | No. of lorises | Sightings/km (±SD) | Subspecies identity |
|---|---|---|---|---|---|---|
| Kottayam | Kumily (1)* | RF | 9 | 3 | 0.05 | ? |
| | Erumeli (2) | RF | 8 | 1 | 0.12 | ? |
| Periyar TR | Thekkady (3) | TR | 24 | 0 | - | - |
| | Vallakadavu (4) | TR | 56 | 1 | 0.03 (±0.09) | *L. l. malabaricus* |
| | Periyar (5) | TR | 19 | 0 | - | - |
| | Azhutha (6) | TR | 12 | 0 | - | - |
| | Pampa (7) | TR | 10 | 0 | - | - |
| Ranni | Goodrickal (8) | RF | 120 | 0 | - | - |
| | Vadasserikkara (9) | RF | 43 | 0 | - | - |
| Konni | Naduvathumuzhy (10) | RF | 10 | 5 | 0.50 | *L. l. malabaricus* |
| | Mannarappara (11) | RF | 1 | 1 | 0.05 | *L. l. malabaricus* |
| Achenkovil | Kallar (12) | RF | 22 | 4 | 0.18 | *L. l. malabaricus* |
| | Kanayar (13) | RF | 20 | 1 | 0.05 | *L. l. malabaricus* |
| | Achenkovil (14) | RF | 51 | 3 | 0.04 (±0.04) | *L. l. malabaricus* |
| Punalur | Pathanapuram (15) | RF | 25 | 3 | 0.07 (±0.11) | *L. l. makabaricus* |
| Thenmala | Thenmala (16) | RF | 8 | 0 | - | - |
| | Arienkavu (17) | RF | 18 | 1 | 0.05 | *L. l. malabaricus* |
| Shendurney | Shendurney (18) | WLS | 22 | 2 | 0.09 (±0.01) | *L. l. malabaricus* |
| Thiruvananthapuram | Kulathupuzha (19) | RF | 40 | 2 | 0.05 (±0.07) | *L. l. malabaricus* |
| | Palode (20) | RF | 32 | 5 | 0.21 (±0.24) | *L. l. malabaricus* |
| | Paruthipally (21) | RF | 12 | 6 | 0.50 | *L. l. malabaricus* |
| Peppara | Peppara (22) | WLS | 48 | 5 | 0.21 (±0.29) | *L. l. malabaricus* |
| Neyyar | Neyyar (23) | WLS | 36 | 4 | 0.12 (±0.14) | *L. l. lydekkerianus* |
| | Total | | **641** | **47** | **0.07 (±0.13)** | |

TR: Tiger Reserve; WLS: Wildlife Sanctuary; RF: Reserve Forest
*Numbers in parentheses indicate location in Figure1.

trails or transects walked or motored was the sample size. In each forest range, the standard deviation for encounter rate was computed when the sample size was more than two. A handheld global position system (GPS) was used to record the location of the animals seen and the distance covered during the survey. For each sighting, we recorded the number of individuals, the subspecies, height from the ground, the substratum and tree species, and the habitat type. Body size, coat color, and shape of the circumocular patches were used to distinguish the Mysore from the Malabar slender loris (Kumara *et al.* 2006). The lorises were observed closely in order to distinguish the identity of the subspecies based on coat color and circumocular patches. We took photographs when we were uncertain of the identity of the subspecies. The surveys were carried out between November 2012 and April 2013, and totaled 641 km by foot and vehicle.

We combined our results with those of an earlier study by Radhakrishna *et al.* (2011) to provide an overall picture of distribution and relative abundance of slender lorises in Kerala.

## Results

### *Distribution and abundance in southern Kerala*

Forty-seven lorises were seen during the 641 km of transects (Table 1). Slender lorises were found in all of the forest divisions except Ranni (Table 1, Fig. 2). The encounter rate varied considerably between the ranges (Table 1); the highest was in Naduvathumuzhy (0.50 lorises/km) in Konni forest division and Paruthipally range (0.50 lorises/km) in Thiruvananthapuram. They were followed by Palode (0.21 ±0.24 SD lorises/km) in Thiruvananthapuram forest division and Peppara (0.21 ±0.29 SD lorises/km) in the Peppara Wildlife Sanctuary. The overall encounter rate was 0.07 ±0.13 SD lorises/km. We were unable to identify four lorises seen in Kottayam forest divisions. All other lorises seen were *Loris lydekkerianus malabaricus*, except the four in the Neyyar Wildlife Sanctuary, which were *L. l. lydekkerianus*.

The relative abundance of lorises in moist deciduous forest (0.31 ±0.16 SD lorises/km) was significantly higher (Kruskal-Wallis, $\chi^2 = 25.32$, df = 2, $p<0.001$) than in evergreen forest (0.02 ±0.06 SD lorises/km) and plantations (0.04 ±0.05 SD lorises/km) (Fig. 3). Of the 47 lorises seen,

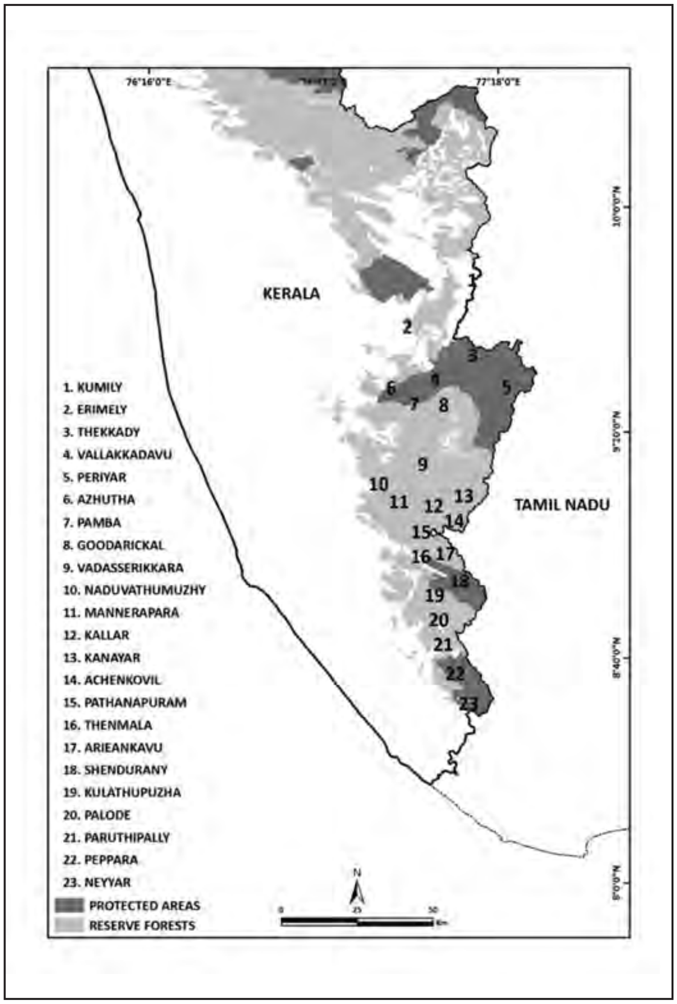

**Figure 1.** Location of forests surveyed for slender loris in southern Kerala.

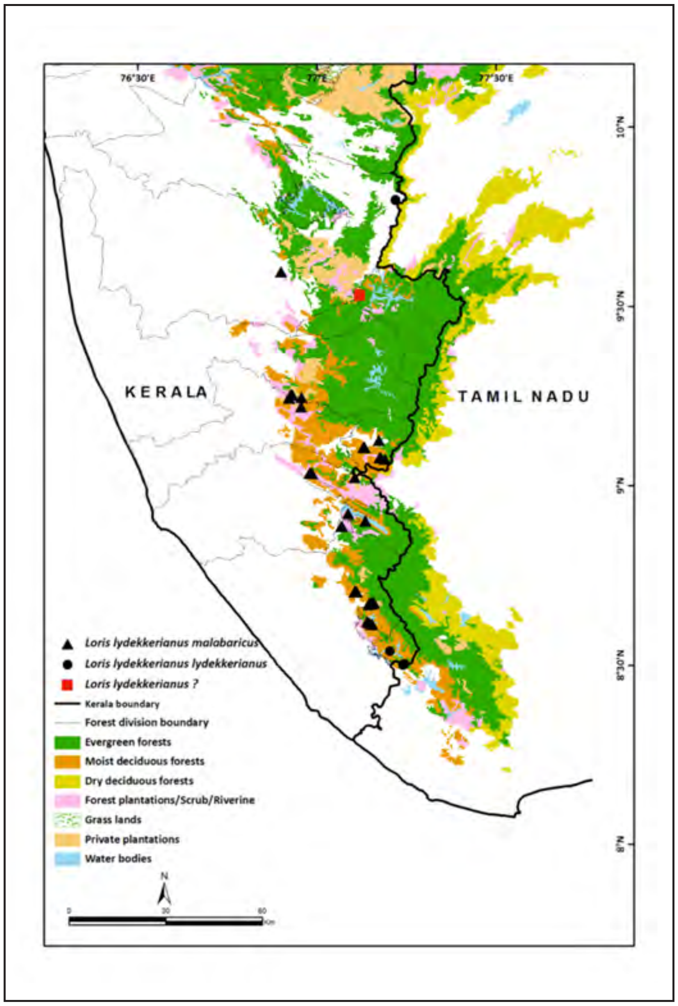

**Figure 2.** Sightings of subspecies of slender loris in southern Kerala.

36 (77%) were at elevations of <300 m above sea level, and 11 (23%) were between 301 and 1200 m (Fig. 4).

*Distribution and abundance in Kerala combining the present survey and that of Radhakrishna et al. 2011*

Slender lorises were found in the forests of the Western Ghats from the Neyyar Wildlife Sanctuary in the south to the Aralam Wildlife Sanctuary in the north (Fig. 5). In spite of a large sampling effort, lorises were not seen in stretches of evergreen forest in the Periyar Tiger Reserve (our data) and Parambikulam Tiger Reserve (Radhakrishna *et al.* 2011). Among all the forest divisions and forest ranges, the highest encounter rate was in Aralam Wildlife Sanctuary (1.44 ±1.07 SD lorises/km), followed by the Chimony Wildlife Sanctuary (0.06 ±0.57 SD lorises/km), the Naduvathumuzhy range (0.50 lorises/km) of Konni forest division, and the Paruthipally range (0.50 lorises/km) in Thiruvananthapuram. The overall encounter rate for the state was 0.12 ±0.31 SD lorises/km.

In southern Kerala, lorises were more abundant in moist deciduous forest, whereas in central and northern Kerala they were found predominantly in evergreen forest. Overall, relative abundances were higher in evergreen forest (0.18 ±0.51 SD lorises/km), followed by moist deciduous forest (0.14 ±0.18 SD lorises/km), dry deciduous forest (0.10 ±0.20 SD lorises/km) and plantations (0.07 ±0.13 SD lorises/km) (Fig. 6). The relative abundance of lorises did not differ significantly, however, across these vegetation types (Kruskal-Wallis, $\chi^2 = 4.17$, df = 3, $p = 0.244$). Lorises were recorded at elevations of 65 to 1871 m above sea level, but 55% of the sightings (N = 81) were at <300 m (Fig. 7). There was no significant difference in the relative abundance of lorises in protected areas (0.14 ±0.40 SD lorises/km) compared to reserve forests (0.11 ±0.18 SD lorises/km) ($t = 0.682$, df = 181, $p = 0.496$) (Fig. 8).

## Discussion

The findings from the present study combined with the data from the surveys of Radhakrishna *et al.* (2011) provide a more complete picture of the distribution and abundance

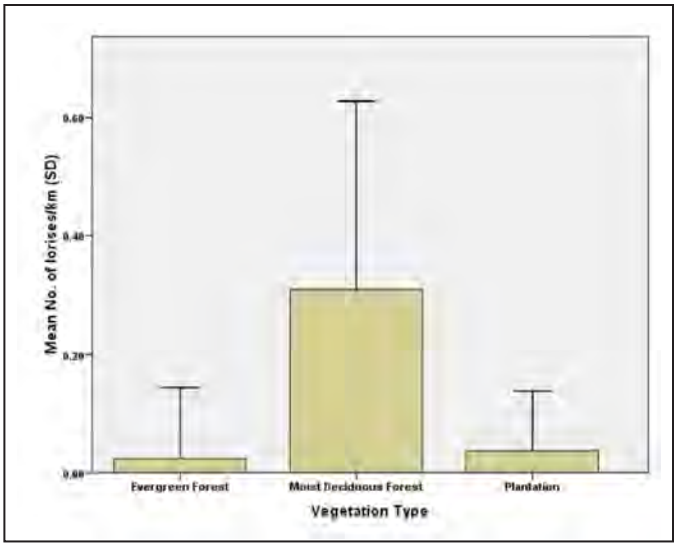

**Figure 3.** Mean number of lorises sighted in different vegetation types of southern Kerala.

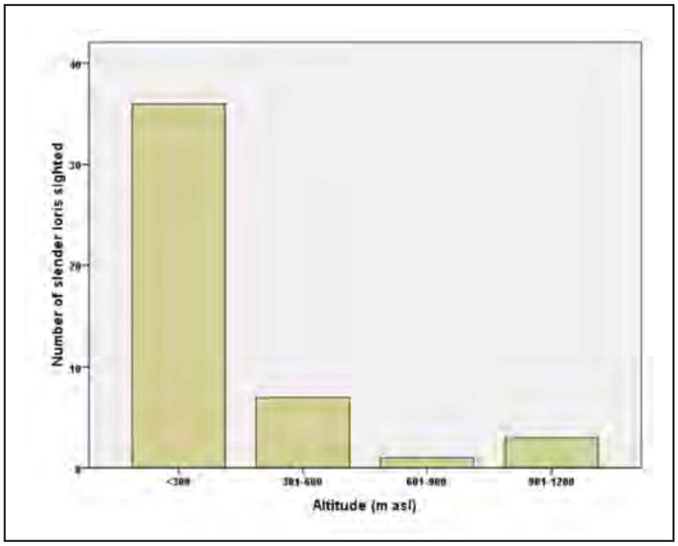

**Figure 4.** Number of lorises seen at different elevations in southern Kerala.

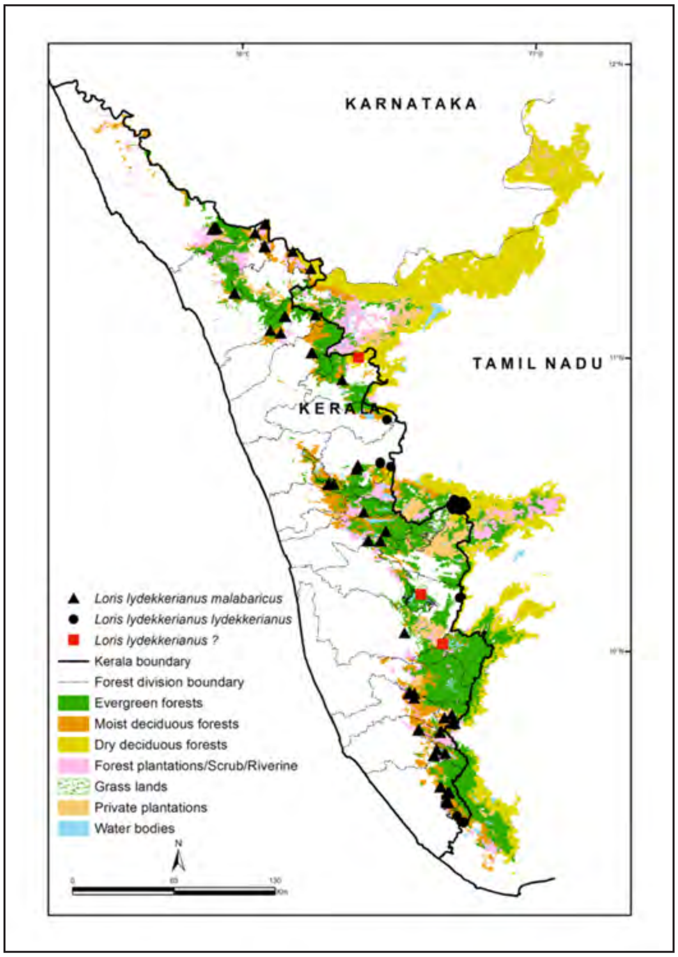

**Figure 5.**Sightings of different subspecies of slender loris in Kerala (from this study and Radhakrishna *et al*. 2011).

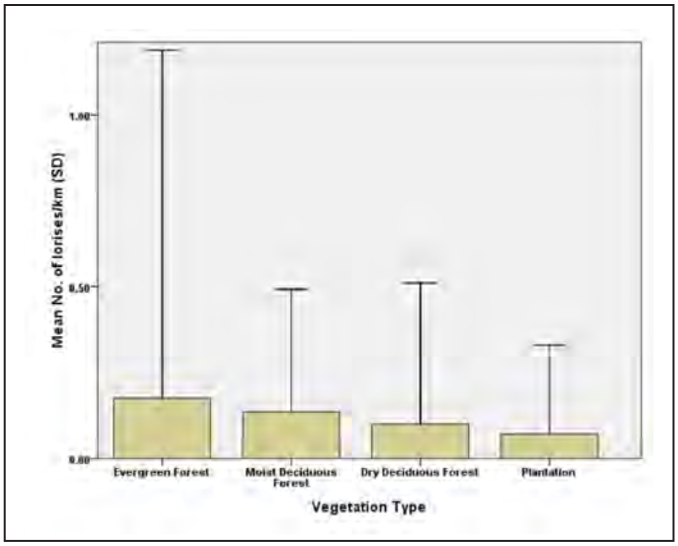

**Figure 6.** Mean number of lorises seen in different vegetation types in Kerala (from this study and Radhakrishna *et al.* 2011).

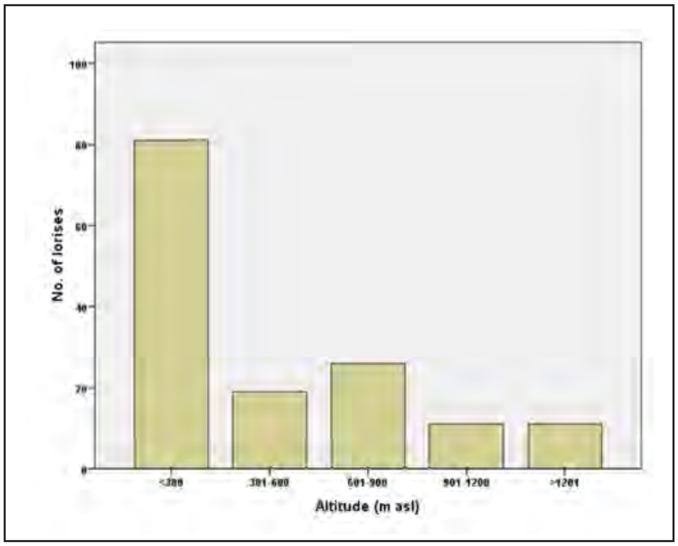

**Figure 7.** Number of lorises seen at different elevations in Kerala (from this study and Radhakrishna *et al.*2011).

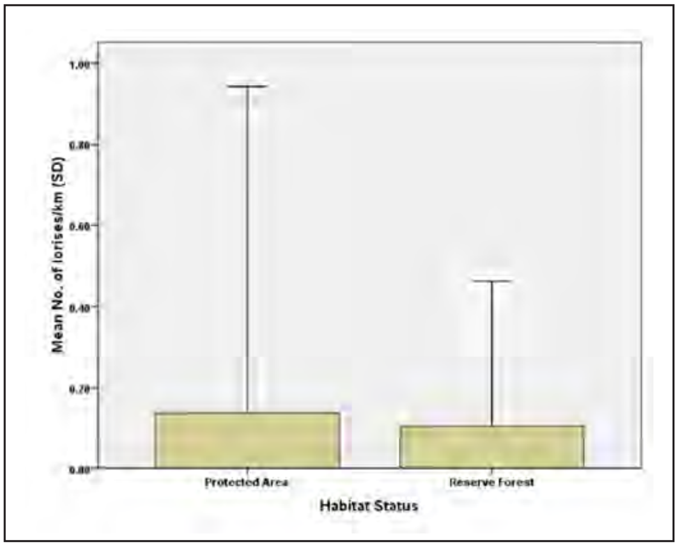

**Figure 8.** Mean numbers of lorises in areas with different protected status in Kerala (from this study and Radhakrishna *et al*. 2011).

of the two subspecies of slender loris in Kerala. The range of *L. l. malabaricus* is evidently confined to the western slopes of the Western Ghats. The Ariankavu pass and the Palghat gap have created a major barrier, resulting in separate populations for *L. l. malabaricus*. For this reason, the population of *L. l. malabaricus* in Kerala should be considered as three subpopulations: (1) lorises in the Neyyar Wildlife Sanctuary in the southern tip to the south of the Ariankavu pass; (2) lorises north of the Ariankavu pass up to south of the Palghat Gap; and (3) those north of the Palghat gap up to the Aralam Wildlife Sanctuary. The population of the Aralam Wildlife Sanctuary is contiguous with the population in Karnataka (Kumara *et al.* 2006).

In spite of considerable efforts, lorises were not seen in the large tracts of evergreen forest in the Parambikulam and Periyar tiger reserves. If there are lorises in these reserves, they would be contiguous through the low elevation forests of the region. Although some reports indicate that lorises occur in these forests (Easa and Balakrishnan 1990; Nameer 2000; Nameer *et al.*2007), there is no evidence based on confirmed sightings. If lorises are present they must be very scarce. Lorises in Kerala are very largely confined to forested areas and department-owned plantations. We presume that they have been eliminated elsewhere, or are at best persisting in very low numbers along the fringes of forests and privately owned plantations and cultivated areas.

The relative abundance of *L. l. malabaricus* in most of the forest divisions of Kerala is <0.2 lorises/km, except at the Aralam Wildlife Sanctuary, Konni, Thiruvanthapuram, Nemmara and Chimmoney. These areas, which had a higher abundance, had degraded evergreen forests with a well-developed shrub layer; probably an important factor that enhances the availability of foods such as insects (Kumara *et al.*2006). However, high abundance should not be adopted as a criterion for planning the conservation initiatives, since they are largely confined to the state's forested areas. The major goal for the protection of Kerala's lorises should be protection of their habitats throughout the state, wherever they occur.

In Kerala, *L. l. lydekkerianus* is confined to forests around the Palghat gap, the Chinnar Wildlife Sanctuary, Kumily Range and the Neyyar Wildlife Sanctuary. These areas have relatively dry forests as they are situated in rain shadow areas contiguous with the dry forests of the eastern slopes. The population in Chinnar Wildlife Sanctuary may be isolated from the nearest population of *L. l. malabaricus*. The population of *L. l. lydekkerianus* present south of Palghat and in the Neyyar Wildlife Sanctuary is, however, contiguous with the population of *L. l. malabaricus*. Further studies on these two populations might throw light on how the ranges of these two subspecies overlap or interdigitate, and their possible hybridization and interactions.

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# Population Status of the Endangered Lion-tailed Macaque *Macaca silenus* in Kalakad-Mundanthurai Tiger Reserve, Western Ghats, India

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**Abstract:** The lion-tailed macaque, endemic to the evergreen forests of the Western Ghats in southern India, is endangered. Over the last two decades surveys have documented population declines in a number of areas. There still exists a huge gap, however, in our knowledge of this macaque's status at many sites. It is imperative to identify and conserve existing populations in contiguous, large and undisturbed forests. We present the results of a first complete population survey carried out in the Kalakad-Mundanthurai Tiger Reserve (KMTR) in the Agasthyamalai landscape; an area that has not been surveyed for two decades. We found a population of at least 462 lion-tailed macaques in 30 groups. The mean group size was 15.4 individuals per group, and the adult sex ratio was 3.5 females/male. The forest of the KMTR is connected with forest reserves in the states of Tamilnadu and Kerala, and it is probable that the lion-tailed macaque population of KMTR is likewise contiguous. Measures must be taken at a landscape level for the long-term conservation of the species; the status of the populations in the neighboring sites need to be assessed, and priority should be given to adequate protection for the Agasthyamalai sub-population as a whole.

**Key Words:** lion-tailed macaque, southern Western Ghats, primate surveys, habitat connectivity, Agasthyamalai landscape

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## Introduction

Primates are among the most imperiled of the mammals (Ceballos and Brown 1995; Schipper *et al*. 2008), with many species occurring in regions of high human density (Harcourt and Parks 2003). Habitat loss and hunting have been the major causes for the population declines of many primate species (Chapman and Peres 2001; Mittermeier *et al*. 2009); many survive in just fragments of their former contiguous habitat, often as small and isolated populations (Mittermeier and Cheney 1987). These threats exacerbate extirpation risks in primate species, especially those with life history traits associated with slow reproductive rates and a limited capacity for population recovery (Isaac and Cowlishaw 2004; Purvis *et al*. 2000). The long-term survival of some primates may hinge on just a few remaining habitats large enough to maintain viable populations (Chapman and Peres 2001; Zeigler *et al*. 2010).

The lion-tailed macaque, *Macaca silenus* (Linnaeus, 1758), is endemic to the Western Ghats in southern India, and is Endangered (Kumar *et al.* 2008). It is a habitat specialist, restricted to the evergreen forests of the Ghats (Singh *et al*. 1997). Being primarily frugivorous with a narrow dietary niche, it requires a perennial fruit availability (Kumar 1987; Sushma and Singh 2006). Its life history traits are typical of a primate adapted to a stable environment, rendering it vulnerable to changes in habitat and to hunting (Kumar 1987). Forest connectivity is important for the dispersal of adult males, as is evident from the unnaturally high proportion of adult males in fragments that lack connectivity (Umapathy and Kumar 2000a).

The geographical area of occupancy of the lion-tailed macaque is less than 2,500 km². It extends from a few kilometers north of the Sharavati River (14°N) in Karnataka (Karanth 1985; Kumara and Singh 2004) to the Agasthyamalai hills (8°N) at the southern tip of the Western Ghats (Green and Minkowski 1977). Presently, it is believed that about 3,500 lion-tailed macaques survive in 49 sub-populations across eight locations (Molur *et al.* 2003). Many of these sub-populations are restricted to fragments that are small and isolated (Singh *et al.* 2002). There are four known sites in its entire range that hold large populations in relatively large forests (Singh *et al.* 2009): (1) Sirsi and Honnavara Forest Divisions in Karnataka (Kumara and Singh 2004); (2) Kudremukh National Park and the adjoining sanctuaries (Kumara and

Singh 2008); (3) Silent Valley National Park (Ramachandran and Joseph 2001); and (4) the Kalakad-Mundanthurai Tiger Reserve (KMTR). While there have been surveys undertaken in the recent past in the first three of these sites, there has been none in the KMTR. Because of the large extent of forest, Molur *et al.* (2003) identified it as a site with the potential of harboring a significant population of lion-tailed macaques. Along with adjoining forests, the KMTR forms the southernmost limit of the macaque's geographic range—the Agasthyamalai landscape. It is also a distinct sub-population with tenuous connectivity at the Shencottah gap (9°) that has a railway line and a national highway passing through it, and is densely populated, with a large number of homesteads and small landholdings (Gangadharan *et al.* 2011). There is unlikely to be connectivity for these macaques across this gap. KMTR is thus deemed to play an important role for lion-tailed macaque conservation in the Agasthyamalai landscape.

Only two reports on the population of lion-tailed macaques in the KMTR were available prior to the present survey. The earliest survey reported 14 groups with 145 individuals (Green and Minkowski 1977). This was followed by a rapid survey that reported 15 groups with 159 individuals (Hohmann and Sunderraj 1990). Both surveys were based on local knowledge and restricted to just parts of the reserve.

During 2008–2009, we carried out a survey to assess the population status of lion-tailed macaques in the KMTR. In this paper we report our findings and discuss the importance of this sub-population for the conservation of the lion-tailed macaque.

## Methods

### *Study site*

The Kalakad-Mundanthurai Tiger Reserve (89,500 ha) is situated at the southernmost end of the Western Ghats on the eastern slopes, 8°25'–8°53'N and 77°15'–77°35'E (Fig. 1). Elevation ranges from 100 m to 1866 m above sea level. This region receives rainfall during the south-west monsoon (June–August) and the north-east monsoon (October–December). Mean annual rainfall is about 3,000 mm.

Forest types in the KMTR range from west-coast, tropical evergreen to semi-evergreen, moist mixed-deciduous, and dry mixed-deciduous, to thorn forest (Champion and Seth 1968). The prime lion-tailed macaque habitat there is wet evergreen forest, which covers about 20,000 ha and is mostly undisturbed (Giriraj *et al*. 2008). There are 28 human enclaves in the reserve. They include Electricity Board settlements and commercial plantations of tea, coconut, clove and cardamom (Ali and Pai 2001). While most plantations are abandoned, two are still functional and are situated in the middle of the Reserve, one of them a tea estate, covering an area of about 3,400 ha. There are also a few scattered human enclaves (Ali and Pai, 2001). Many of the abandoned plantations were acquired by the Reserve in 1995 and allowed to regenerate into forest (Ali and Pai 2001). The KMTR, along with other adjoining parks and reserves in Kerala and Tamil Nadu, form the Agasthyamalai landscape, which has some of the least fragmented forest stretches in the southern Western Ghats.

### Data collection

In order to cover the study area systematically, we overlaid a grid of 2.23 × 2.23 km cells on the vegetation map of KMTR using ArcView Version 3.2 (Environmental Systems Research Institute, Inc. California). We chose this cell size since it approximately equals the average home range size of a lion-tailed macaque group in the study area (about 500 ha; Green and Minkowski 1977). We selected all cells that contained evergreen forest; the habitat of the lion-tailed macaque. We sampled 40 of 83 selected cells, covering 200 $km^2$, using the existing network of trails and animal paths. The remaining cells were inaccessible due to rough terrain or impenetrable reed brakes. Given limited resources and time, we did not attempt to cut transects. The average length of the trail walked in each cell was 2.72 km (SD ± 1.02). We used temporal replicates (four consecutive days) to survey each cell, but due to logistic constraints this was not possible for all. We surveyed 23 cells for four days each, eight cells for three days each, two cells for two days each and seven cells were surveyed on just one day. We uploaded the cell locations using DNR GARMIN software (version 5.04) into a handheld GPS (Garmin eTrex VistaHCX), which helped us locate the cells on ground. All surveys were carried out between 0700 h and 1600 h. Each survey was carried out by two people, at least one of them an experienced observer (biologist/trained volunteer). All volunteers were given prior training. All survey teams included one forest-dweller who was familiar with the study area and its fauna. This was done to ensure that the detectability of lion-tailed macaques in the surveys was high and uniform across the cells. Each team walked at a pace of about 1 km/h, scanning the canopy and stopping every few minutes, at intervals of about 30 m, to listen for calls. Three other diurnal arboreal mammals share the habitat with the lion-tailed macaque: the Nilgiri langur (*Semnopithecus johnii*), the bonnet macaque (*Macaca radiata*), and the Indian giant squirrel (*Ratufa indica*). Calls of these species are very different from those of lion-tailed macaques, and hence easily distinguishable. When the team heard a call or detected movement in the canopy away from the trail, the team took a few minutes to leave the trail in order to observe the species. This ensured that there were no false detections. On sighting lion-tailed macaques, we recorded (i) the location using GPS, (ii) the number of individuals, and (iii) date and time. Most of the groups we encountered were not habituated and therefore did not allow observers to follow them in close proximity. Given the rugged terrain and shyness of the groups, it was not always possible to follow the groups to obtain a count. Due to the large group spread typical of lion-tailed macaques (over about 150 m; Kumar 1987), the team counted only when the group made a coordinated movement across a gap in the canopy. There are often stragglers in groups, so we waited for at least 15 minutes after the group had moved to

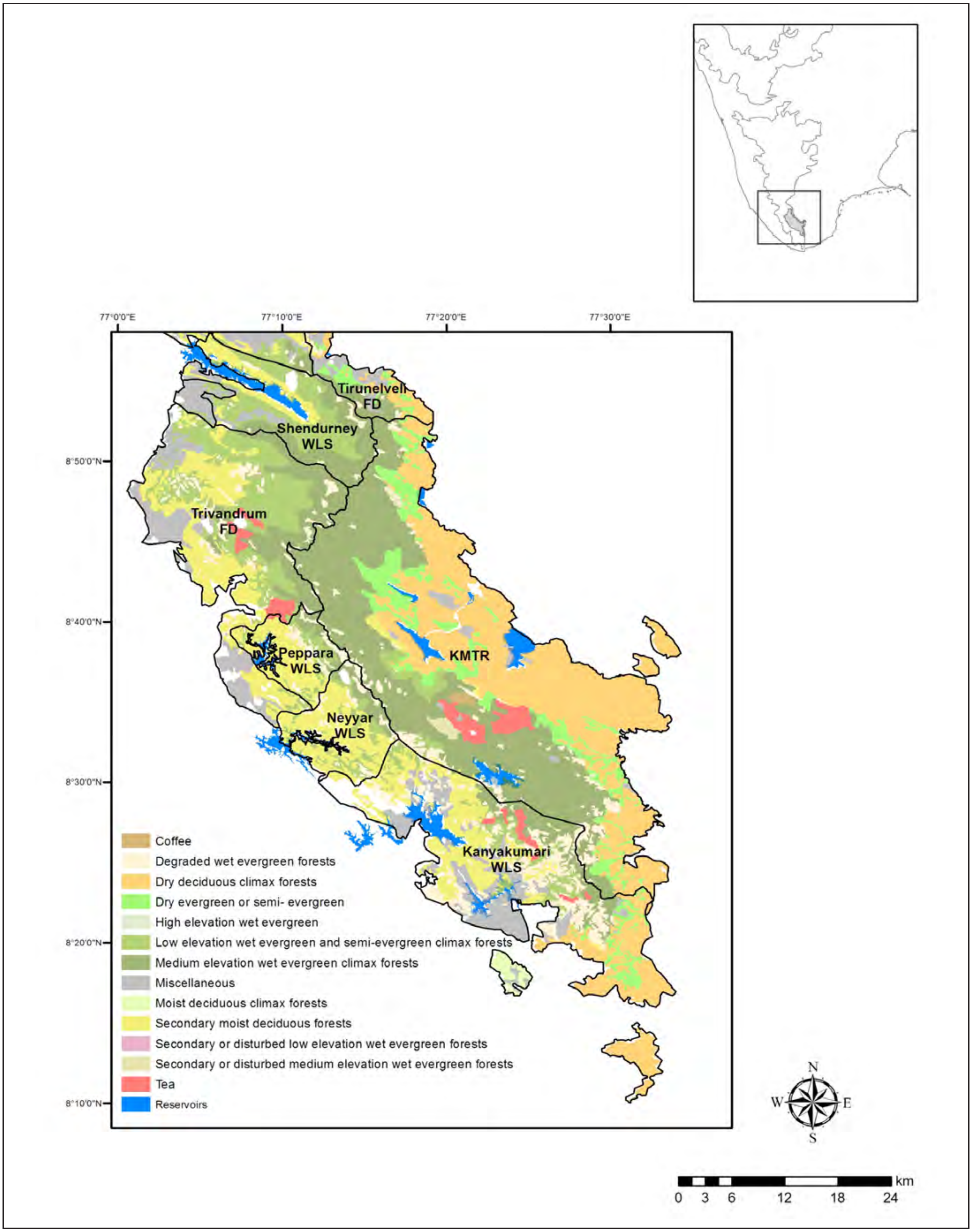

**Figure 1.** Map showing the Agasthyamalai landscape consisting of the Kalakad-Mundanthurai Tiger Reserve (KMTR) and adjoining areas and different vegetation types in the landscape. Inset map shows Western Ghats with the study area (KMTR) at the southern tip of India (Vegetation map attribution: B. R. Ramesh, D. De Franceschi and J.-P. Pascal, French Institute Pondicherry, downloaded from http://thewesternghats.indiabiodiversity.org).

**Table 1.** Group structure of lion-tailed macaque groups in the Kalakad-Mundanthurai Tiger Reserve.

| Group | Size | Adult male | Adult female | Subadult | Juveniles | Infants | Immature | Unidentified |
|---|---|---|---|---|---|---|---|---|
| Sengaltheri CE | 10 | 1 | 5 | 0 | 1 | 2 | 3 | 1 |
| Oothu | 22 | 2 | 9 | 0 | 10 | 1 | 11 | 0 |
| Peyar | 16 | 2 | 7 | 0 | 4 | 1 | 5 | 2 |
| Knapp's hut | 20 | 2 | 7 | 1 | 5 | 5 | 10 | 0 |
| 8th mile | 12 | 1 | 5 | 0 | 4 | 2 | 6 | 0 |
| Valayar CE | 14 | 2 | 5 | 3 | 3 | 1 | 4 | 0 |
| Manimutthar | 13 | 2 | 4 | 1 | 2 | 2 | 4 | 2 |
| Total | 107 | 12 | 42 | 5 | 29 | 14 | 43 | 5 |
| Mean |  | 1.71 | 6 | 0.71 | 4.14 | 2 | 6.14 |  |

ensure that all the individuals were counted. The survey was then resumed from the spot from where the team deviated. Whenever we failed to get a full group count, we revisited these cells to locate the groups again. Information on group composition was recorded only when we were certain that all the animals in group were identified unambiguously. Only two researchers who had prior experience of studying lion-tailed macaques were involved in collecting information on group composition. We followed Kumar (1987), using body size and morphological features to distinguish individuals of different age-sex categories. In order to arrive at the number of groups and avoid double counts, we adopted the method described in Kumara and Singh (2008). We counted any two detections of LTM in a survey as distinct groups if they occurred >1.3 km apart, or <1.3 km but <1 h apart. We arrived at a minimum number of groups by pooling all identified in this way, along with incidental sightings that did not violate the criteria laid down for the survey. The field surveys were carried out between October 2008 and September 2009.

## Results

The total length of the trails used for sampling was 108.7 km, and the total sampling effort, including replicates, was 347.5 km. The estimation of sampling effort did not include the distance traveled away from the trail while following monkeys. We saw lion-tailed macaques 48 times during our survey. Mean encounter rate was 0.14 groups/km (SE ± 0.02). They were found at elevations ranging from 370 m to 1300 m above sea level.

We were able to distinguish 30 groups of lion-tailed macaques (Fig. 2). However, secondary information from reliable sources (such as other researchers working in the reserve) revealed the presence of four other groups. We also saw solitary adult males on three occasions in different areas of the reserve. We obtained group size information from 15 of the groups (see Appendix). The mean group size was 15.4 individuals (SD ± 3.24; 95% CI 13.04–17.75). We estimate a minimum number of 462 individuals in 200 km². The group composition for seven groups is shown in Table 1. The mean numbers of males and females per group were 1.71 and 6, respectively. Overall, the adult male–adult female sex ratio was 3.5 females per male. The adult female–immature ratio was 1:1.02, and the adult female–infant ratio was 1:0.3 (Table 2).

**Table 2.** Age-sex ratios of lion-tailed macaque groups in the Kalakad-Mundanthurai Tiger Reserve.

| Age-Sex | Number of individuals | Ratio |
|---|---|---|
| Adult ♂ : Adult ♀ | 12 : 42 | 1: 3.5 |
| Adult ♀ : Immature | 42 : 43 | 1: 1.02 |
| Adult ♀: Infant | 42 : 14 | 1: 0.33 |

## Discussion

Conserving lion-tailed macaques will require providing protection for the habitat and populations (Singh *et al*. 2009). Gaps in our knowledge of population status at many sites and the lack of a systematic monitoring program are impediments to the *in situ* conservation of this species. Although we could not survey all of the lion-tailed macaque habitat in the KMTR, we can indicate a minimum population size of at least 30 groups with 462 individuals. This is much higher than the previous population assessments for the KMTR (Green and Minkowski, 1977; Hohmann and Sunderraj, 1990). While the methods used in the three surveys were different and cannot be compared, the higher estimate in our survey is due to enhanced effort, covering areas that had not been surveyed before. Threats faced by populations at other sites are not prevalent in the KMTR, making it singularly important for lion-tailed macaques. The Sirsi-Honnavara population is within unprotected, multiple use forests that are interspersed with fields, and faces encroachment and degradation of its habitat (Kumara and Sinha 2009). Hunting has led to population declines even in protected areas such as Kudremukh National Park (Kumara and Sinha 2009). Populations in Kerala also suffer poaching (Molur *et al.* 2003). However, habitat degradation, mainly through fire, and, to a lesser degree, degradation of forests close to human enclaves such as the tea estate are threats in the KMTR (Annamalai 2005). Nearly 16% of the evergreen forest cover has been degraded in the last 25 years in the KMTR (Giriraj *et al.* 2008). Selective logging and encroachment in the past, along with recurrent fires, have led to the proliferation of *Ochlandra* reed brakes in the gaps, preventing the regeneration of trees (Giriraj *et al*. 2008). Enhanced protection, patrolling around human enclaves and

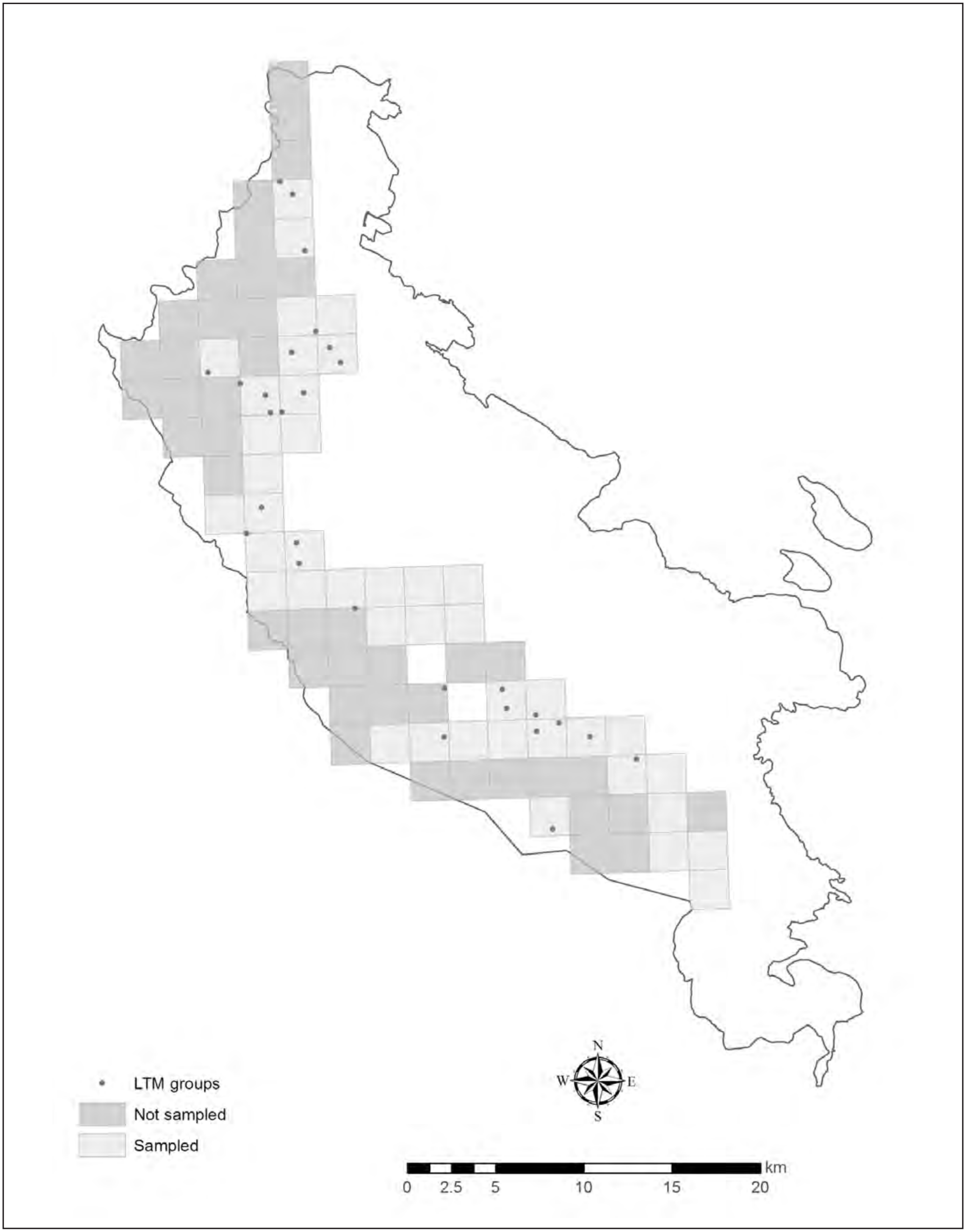

**Figure 2.** Map showing cells that were sampled, not sampled and locations of lion-tailed macaque troops in the Kalakad-Mundanthurai Tiger Reserve (KMTR), Two white cells in the middle of the map cover the tea estate in the reserve.

along the western park boundary, and assisted regeneration of forests in some of the abandoned plantations will be a few important steps towards conservation of lion-tailed macaque and its habitat in the KMTR.

*Conservation priorities for the Agasthyamalai sub-population*

Frugivorous primates such as the lion-tailed macaque, which depend on patchy resources, may be particularly vulnerable to habitat disturbance (Bicknell and Peres 2010; Rode *et al.* 2006). Habitat conservation at the landscape level should be prioritized because landscape attributes and patch characteristics and quality determine the persistence of primates in forest patches (Arroyo-Rodrigues *et al*. 2007; Bicknell and Peres 2010; Umapathy and Kumar 2000b).

The KMTR population is likely to be contiguous with LTM groups in adjoining protected areas (Shendurney, Peppara and Neyyar wildlife sanctuaries) and reserved forests in Kerala as well as the Kanyakumari Wildlife Sanctuary in Tamilnadu, forming the Agasthyamalai sub-population. The current status and distribution of lion-tailed macaques in these sites are, however, not known.

The KMTR is the largest protected area in the Agasthyamalai landscape. It has retained large stretches of pristine habitat and a viable lion-tailed macaque population, giving it a key role in the long-term persistence of the species. The challenge for the conservation of the lion-tailed macaque in this landscape is to identify, monitor and restore connectivity between the KMTR and the surrounding forest reserves. This requires a larger, species-specific conservation plan to be drawn up by the two states, Kerala and Tamilnadu, targeting the entire landscape. Population assessments in the neighboring state forests need to be carried out at regular intervals, and adequate protection needs to be provided for these groups. Given the anthropogenic pressures on native forests in the Western Ghats (Davidar *et al*. 2010), habitat monitoring, using both remote sensing techniques and ground assessments, should be a priority. The prospects of conserving this endangered macaque pivots on identifying large populations, monitoring them, and providing the necessary protection.

## Acknowledgments

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**Appendix:** Lion-tailed macaque troops and their sighting locations in the Kalakad-Mundanthurai Tiger Reserve.

| No. | Group identity | Group size | Administrative Range |
|---|---|---|---|
| 1. | Karupusami Koil 1 | ? | Kadayam |
| 2. | Karupusami Koil 2 | 10 | Kadayam |
| 3. | Nondimankadu | 13 | Kadayam |
| 4. | Chinnapul 1 | ? | Mundanthurai |
| 5. | Udumbukal 2 | ? | Mundanthurai |
| 6. | Valparai | ? | Mundanthurai |
| 7. | Kodamadi 1 | ? | Mundanthurai |
| 8. | Kodamadi 2 | ? | Mundanthurai |
| 9. | Valukku odai | ? | Mundanthurai |
| 10. | 8th mile 2 | 12 | Mundanthurai |
| 11. | Knapp's hut | 20 | Mundanthurai |
| 12. | Valayar CE | 14 | Mundanthurai |
| 13. | Kandaparai | ? | Mundanthurai |
| 14. | Peyar | 16 | Mundanthurai |
| 15. | Kannikatti | 21 | Mundanthurai |
| 16. | Injikuli | ? | Mundanthurai |
| 17. | Pambar | ? | Mundanthurai |
| 18. | Mylar 1 | ? | Mundanthurai |
| 19. | Mylar 2 | 16 | Mundanthurai |
| 20. | Thenparai 1 | 12 | Papanasam |
| 21. | Thenparai 2 | ? | Papanasam |
| 22. | Oothu CE | 22 | Amb/BBTC |
| 23. | Manimuthar 1 | ? | Ambasamudram |
| 24. | Manimuthar 2 | 13 | Ambasamudram |
| 25. | Kakkachi 1 | 16 | Ambasamudram |
| 26. | Kasunguliar 1 | ? | Ambasamudram |
| 27. | Kodayar | 25 | Kodayar |
| 28. | Kakkachi 2 | ? | Kalakad |
| 29. | Kasunguliar 3 | 11 | Kalakad |
| 30. | Sengaltheri CE | 10 | Kalakad |

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# Population Dynamics of a Reintroduced Population of Captive-Raised Gibbons (*Hylobates lar*) on Phuket, Thailand

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**Abstract:** Confiscated and donated white-handed gibbons (*Hylobates lar*) originating from the local wildlife trade have been rescued by the Gibbon Rehabilitation Project (GRP) and rehabilitated on Phuket since 1992. Here we present some results of this long-term gibbon reintroduction project. Following unsuccessful early release attempts beginning in 1993, GRP has experimented with reintroduction methods and developed a protocol that has succeeded in re-establishing a small independent breeding population in a 22-km$^2$ forest fragment on Phuket. Eight breeding families of gibbons were released into the Khao Phra Thaew non-hunting area between October 2002 and November 2012 using a soft-release reintroduction method in which the gibbons were provisioned with fresh food in the trees for at least one year, or as long as they needed it. The adult pair in the first gibbon family that was reintroduced there has remained together for 10 years post-release, they have maintained the original pair-bond and raised three wild-born offspring. The reintroduced population has seen eleven infants born in the wild, including a second-generation gibbon born to the first wild-born female. Female interbirth intervals and ages at first reproduction in the reintroduced population are comparable with those in wild populations. Of the seven adult females originally released, two remain with their original mates and two remain in the wild paired with different mates. By the end of 2012, three of the six wild groups were not nuclear families, indicating a flexibility of group composition seen in well-studied wild populations.

**Key Words:** Gibbon, *Hylobates lar*, rehabilitation, reintroduction, white-handed gibbon, wildlife trade

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## Introduction

The threats that gibbons are facing from habitat degradation are strongly exacerbated by pressure from the flourishing illegal wildlife trade for pets, entertainment, and traditional medicine (Nijman *et al.* 2009). All but one species of gibbon are now listed as Endangered or Critically Endangered on IUCN's Red List (IUCN 2008), and without targeted conservation efforts several species of gibbons may face imminent extinction (Melfi 2012).

Conservation measures often suggested to help save threatened and declining populations from extinction are different forms of conservation translocations (Wilson and Price 1994; Molur *et al*. 2005: IUCN 2013). However, the potential species conservation benefits of primate translocation projects are perhaps often exaggerated, and translocation projects should not be judged solely on this criterion (Cheyne 2009b; Osterberg *et al*. in press). We start with a quick review of the history of primate conservation translocations.

To date, the successful population restoration of the small golden lion tamarin in Brazil (Beck *et al.* 1994) is the only example from the primate world where released animals have survived in large enough numbers to breed and boost declining wild population numbers (Beck 1995; Cowlishaw and Dunbar 2000). Recent conservation translocation projects with great apes have resulted in high individual survival for released animals (*Pan troglodytes*: Goossens *et al*. 2005; *Gorilla gorilla*: King and Courage 2008; King *et al.* 2012), but because of the apes' longer life history it remains too early to say whether these attempts will help boost wild populations and thus become significant for species conservation.

No equivalent results have been reported on gibbons to date. Because the illegal wildlife trade in Asia has for a long time posed a considerable threat to wild gibbon populations in many range countries (Cheyne *et al.* 2008; Nijman *et al.* 2009), it was once not unusual that gibbons were released from overcrowded holding facilities without appropriate rehabilitation (Indonesia: Bennett 1992; Cheyne 2004; Thailand: Eudey 1991–1992). The continued pressure on government facilities and NGOs to accommodate the growing numbers of animals coming in from the wildlife trade is often the reason behind hasty decisions to release confiscated wildlife without conducting appropriate pre-and post-release work. The truth is that the financial costs of appropriate rehabilitation programs for long-lived primates such as gibbons can be extremely high (Kleiman 1996; Cheyne 2009a). Many past gibbon release projects have been heavily criticized because of high animal mortality or lack of post-release monitoring (Loftin 1995; Ware 2001; Cheyne 2009b). Many such release efforts we are aware of have not been documented or even reported.

The earliest documented release program in Thailand was carried out by the SEATO Medical Research Laboratory in the 1960s, aimed at establishing a sustained supply of gibbons for medical research on an island in the Gulf of Thailand (Berkson *et al.* 1971; Brockelman *et al*. 1973, 1974). Although the project was not directly aimed at achieving conservation goals, it nevertheless proved that captive-raised adult pairs released into the wild can survive and reproduce. It yielded other findings important to later population restoration efforts—captive-raised gibbons tend to assume the same monogamous pair-bonding and aggressive territorial behavior as those in the wild (Carpenter 1940; Ellefson 1974). But the gibbons did not reproduce fast enough to support experimental medical research, and their use for this purpose was discontinued around 1976. The Laboratory then decided to release its remaining gibbons in a forested area in Kanchanaburi Province. The effort was poorly monitored, and its success could not be properly evaluated (Tingpalapong *et al.* 1981). A total of 31 animals were released, and most simply disappeared over the 9-month period in which follow-up observations were made.

In 1991, the groundwork was being laid for the establishment of the GRP in Phuket when the IUCN Captive Breeding Specialist Group and Thai Royal Forest Department (RFD) sponsored a gibbon Population and Habitat Viability Analysis (PHVA) workshop in Thailand (Tunhikorn *et al.* 1993). It had been realized that poaching continued to pose a threat even to large gibbon populations in protected areas (Brockelman 1993–1994) as the growing protected area system in the country did not succeed in offering protection from hunting (for example, Vandergeest 1996). In 1992, a new law required all owners to register their captive gibbons (Tunhikorn *et al.* 1993), but the illegal trade for pets and for tourist photo props continued undiminished. The high numbers of white-handed gibbons in rescue centers around the country provided opportunities for the establishment of reintroduction projects (Eudey 1991–1992; Tunhikorn *et al.* 1993).

The GRP was thus founded in 1992 by the chief RFD officer in Phuket at the time together with an American zoologist. Although administered under the Wild Animal Rescue Foundation of Thailand (WARF) since 1994, the GRP was also closely affiliated with the Wildlife Conservation Division of the Royal Forest Department (later included in the new Department of Parks, Wildlife and Plant Conservation), but managed and implemented largely by an appointed director with the help of international volunteers. The GRP's education and reintroduction program has operated continuously to the present.

The GRP initially began releasing gibbons in a forest on Phuket, but the released animals wandered out of the forest into farmland and human settlements in search of food and human companionship. The project then chose to release gibbons on islands off the coast of Phuket in Phang Nga Bay, as an intermediate step in their rehabilitation prior to release into natural gibbon habitat (Kamerich 2000). In the first attempts both immature and adult gibbons were released in social groups or adult pairs on several small islands between 1993 and 1995. Problems were encountered that limited the success of the releases: weak pair bonds between adults, inadequate area of some of the islands, inadequate food provisioning (most islands were rather remote), and lack of security from humans and their pet dogs. Of the 13 animals released initially, 12 disappeared and were presumed to have died from stress, dog attacks or perhaps being shot by loggers (Breuker 1996). It was subsequently decided to reattempt reintroduction of gibbons on Phuket, following the guidelines of the PHVA workshop (Tunhikorn *et al.* 1993) and IUCN guidelines for non-human primate reintroductions (Baker 2002).

In order to mitigate the poaching of reintroduced animals, the GRP has been carrying out all-important education work in the local schools surrounding the release site, as well as educational projects aimed at international tourists. The latter educational efforts were designed to combat the illegal gibbon trade in Phuket's tourist areas. The GRP was not designed as a species conservation project, but rather grew from an animal welfare need. The project objectives remain to rehabilitate gibbons from the pet trade and tourist industry, to reintroduce suitable candidates back to the wild, and to educate the community at large about gibbons and the forest environment. In the process, a small reproducing population of gibbons has been re-established in the largest forest fragment on the island of Phuket.

We thus describe a conservation translocation effort aimed at re-establishing a viable population of the focal species within its indigenous range (IUCN 2013) and we do this by presenting a case study from the longest-running gibbon reintroduction program to date—The Gibbon Rehabilitation Project (GRP) in Phuket.

## Methods

### *Study area*

The Khao Phra Thaew Non-hunting Area (KPT), established in 1980, protects the largest remaining forest area on Phuket Island, including about 2,228 ha of tropical semi-evergreen forest. The area is surrounded by rubber plantations, villages and roads. The forest area covers steep hillsides 5–500 m above sea level. 8°03'N, 98°24'E (Rawasi 2004) (Fig. 1). Almost no large wildlife has survived the poaching; white-handed gibbons were last seen in the early 1980's.

Forest rangers of the Department of National Parks, Plant and Wildlife Department (DNP) currently patrol the area to prevent hunting and logging.

*Reintroduction methods*

All the gibbons arriving at the GRP are wild-born and either confiscated or donated from the illegal trade in which they are sold for photo props or pets. Over the years, quite a number of gibbons have also been born at the GRP, and many of these first generation captive-born animals have been released before maturity as dependent offspring in a family group. All gibbons that are not participating in the reintroduction program are prevented from breeding. Individuals are excluded from the reintroduction program for any of the following reasons: they have tested positive for diseases, such as Hepatitis B, Tuberculosis, Herpes Simplex Virus or HIV during their initial 90-day quarantine (Punnadee 2006); they belong to a non-native species of gibbon; or they exhibit either physical or psychological trauma. In 2012, 19 (35%) of GRP's 54 captive gibbons were judged to be unsuitable for participation in the reintroduction program (Osterberg *et al*. in press).

After passing their health screening and psychological assessment, gibbons are moved from the quarantine site to the rehabilitation site, located at Bang Pae waterfall by one of the entrances to the KPT forest. There the young gibbons are socialized in large play-groups, and older individuals are found compatible mating partners by introducing them to mature and available, opposite-sex indidvuals. All direct human contact is stopped. Once the gibbons have formed a strong pair-bond, duetted, copulated, and raised at least one offspring successfully past infancy, the family is included in the reintroduction program.

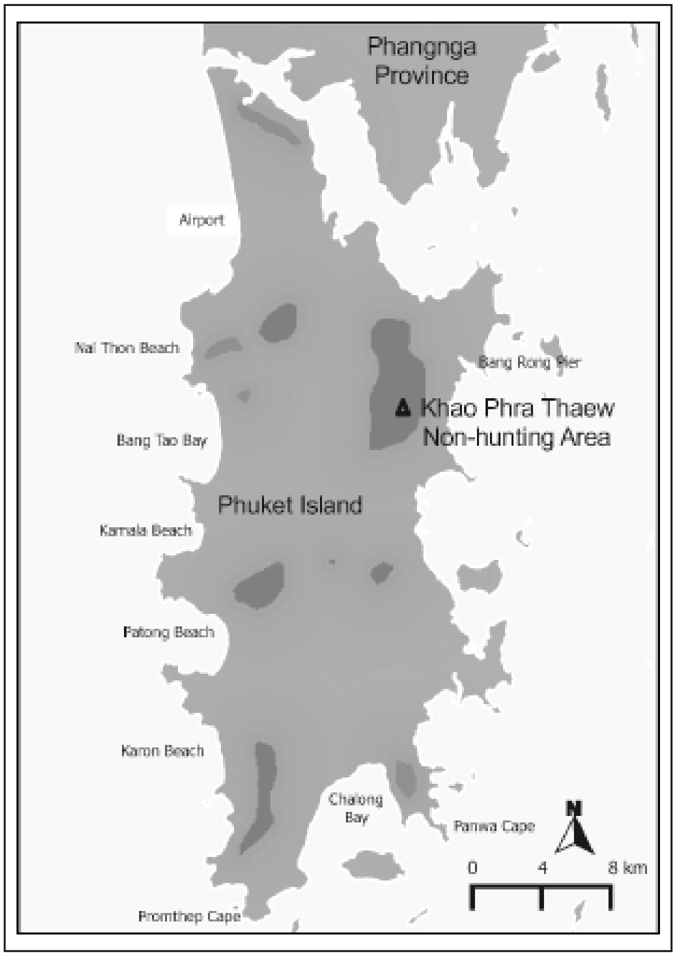

**Figure 1.** Location of Khao Phra Thaew non-hunting area on Phuket.

Since 2002, GRP's aim has been to release one gibbon family per year. Occasional delays to this plan have been due to insufficient volunteer availability, and in some recent years also the lack of available gibbon families. Before each release, a suitable territory for the new family is selected in the KPT forest, and a grid of trails, spaced 50 m apart, is cut around the release site. Once a detailed release plan has been made, a "training cage" is built in the forest. The selected gibbon family then spends its last 3–4 months in captivity there, getting used to the sounds and smells of the forest. GRP staff go into the forest once a day to feed the family.

Initially, the release procedure also included the use of a smaller "acclimatisation cage", made out of nylon mesh and hoisted about 10 m into the forest canopy in the territory selected for the family. The acclimatisation cages were only used in the 5–7 days immediately pre-release, thus preparing the gibbons for a life at greater heights. Five out of eight releases (2002, 2003, 2004, 2006 and 2009) have used this technique. For the 5th release in 2007 the selected territory had to be abandoned, and a new training cage was quickly built farther inside the forest, as another family (released 2003) suddenly expanded their territory in the direction of the first training cage and fought with the family inside. No acclimatisation cage was built after the change of location. In the last two releases this laborious process was abandoned as unnecessary since the gibbons were encouraged to climb higher after release just by feeding them high in the trees. Food is supplied post-release in a basket pulled into the canopy with a rope. By using several alternate feeding stations, and by moving these farther into the family's intended territory, the animals are encouraged to explore and expand their homerange. Feeding has continued for more than a year for all released families. The importance of post-release food provisioning is discussed in detail in Osterberg *et al.* (in press).

All released gibbons have been followed and observed after release. During the first few weeks after release, alternating teams of volunteers and staff carried out all-day focal-animal sampling (Altmann 1974). After the gibbons' initial 2–4 week acclimatisation, observations were made *ad libitum* daily for at least a year, but usually longer. In order to reduce human presence around the released animals, all-day observations were generally avoided after the first month, but the reintroduced population continues to be checked upon by GRP staff indefinitely, as this is the only way to determine reintroduction success as well as follow social and family developments over time. For more details on GRP's post-release monitoring methods see Osterberg *et al.* (in press).

In this paper we present demographic data on births, deaths, infant survival, interbirth intervals, ages at first reproduction, pairbond maintenance, and other observations of importance to the dynamics and survival of the reintroduced gibbon population on Phuket.

## Results

Below we list all groups present at the end of this study and summarize the history of each. Released groups that have disintegrated or merged with other groups are mentioned only where they have been of relevance to the current group compositions. All groups are named after the breeding adult female.

*Kip's family* consisted of the bonded pair and their 2-year-old son at the time of release on 5 October 2002. The adult pair has remained together and has to date raised three wild-born babies past infancy in the wild (Fig. 2). Their captive-born son was translocated from KPT in 2012. The first wild-born baby in Kip's family, named Hope, dispersed from her natal group in 2011 and became a mother to the first second-generation wild-born infant in September 2012.

**Figure 2.** Adult female Kip, released with her mate and one captive born son in 2002, pictured with her third wild-born offspring Omyim in 2010. Photograph by Phamon Samphanthamit.

*Lek's family* was released with two dependent young (Dao and Arun) on 15 August 2003. Lek's mate failed to adjust to the wild and when, by early 2005, he had returned to the rehabilitation site seven times, no further attempts were made to return him to his family. Lek subsequently formed a new pair with a subadult male who was released without a family in the hope that he might pair with the lone female. Lek also adopted the juvenile male offspring, Yoge, released in 2004, upon the disappearance of his parents, whilst she rejected his older sister. Lek, her two biological offspring and the two new family members remained together until the dispersal of all the young between 2008 and 2011. Since 2011, Lek has lived in a nuclear family with her new mate and their wild-born son.

The family currently known as *Dao's family* was released under the name of *Nuan's family* with two dependent offspring on 26 September 2007. After the disappearance of the adult male a year later, maturing female Dao from Lek's family fought with the adult female, Nuan, in order to claim her son Payu as a mate. Nuan was injured and returned to GRP, whereas Dao and Payu became a breeding pair that has given birth to two wild-born offspring. Dao adopted Payu's younger sister who has remained with the group.

*Jita's family* was released with one infant offspring (Claire) on 10 December 2009, and the group was renamed *Hope's family* after both the adults "failed" their reintroductions (Jita disappeared in 2011 and her mate Tony had to be recaptured 3 years post-release in November 2012 after repeatedly showing aggression towards humans). After Jita's disappearance, the father and daughter merged with a young, wild couple: Hope (the first wild-born from Kip's family) and her mate Yoge (the adopted male from Lek's family). Claire remained as an adopted juvenile with this family after her father's recapture.

*Kushta's family* was released on 27 April 2011. In fact, this was Kushta's, and her now 7-year old son's, second release following an unsuccessful attempt in 2006 when Kushta's mate immediately disappeared and Kushta and her young son were returned to GRP. In 2011, Kushta's family consisted of the adult female with her two biological offspring from two different previous pairings, and an adolescent male playmate of the older of these offspring. Although this unrelated young male copulated with Kushta prior to release and conceived an infant with her, he was too immature to act as the group's adult male, and their newborn infant was probably subsequently attacked and killed by "wild" male Arun (the captive-born infant in Lek's family) after the family's release. Kushta's juvenile daughter was also attacked by Arun and had to be returned to the GRP.

*Cop's family* was released with one juvenile offspring on 18 November 2012. The family is so far adapting very well to the wild; they remain a close unit and stay high in the canopy. They were observed singing together for the first time in the wild just six days after release (although Cop did not produce a great call at that time).

In total, eight gibbon families and two sub-adult males—30 gibbons—have been released into the KPT forest since 2002. The success rate of the individual reintroductions has been high. The first family, released in 2002, gave birth to their first wild-born offspring in 2002 and still survives at the release site. In 2003, after the release of a second family, all seven captive-raised animals as well as the wild-born infant were doing well. However, between 12 and 18 months post-release, the ex-pet adult male in the second family made seven voluntary returns to the GRP rehabilitation site and was recaptured and returned to a cage (Table 1).

This male started exhibiting such wandering behavior after conflicts with the male in the first family. All subsequently released families have similarly faced potentially aggressive confrontations with already-established groups in the forest. In August of 2012, the adult captive-born son of the first family was recaptured and translocated to another forest after he failed to acquire a mate in the reintroduced population and started returning to the rehabilitation site and trying to fight with captive males over their female partners. Until his recapture nearly10 years post-release, the first family exhibited 100% reintroduction success, having increased their numbers with three wild-born infants and, in September 2012, also a second generation wild-born. Ten years after the first release, 16 (53%) of the 30 captive-raised gibbons that had been reintroduced still survived in the forest. One gibbon was translocated to another forest and remained wild. Eight gibbons (27%) were returned to captivity for various reasons. The two gibbons that have been released twice are both included as two separate releases, once in the 27% that were returned to the GRP and once as part of the 53% that now appear to be adjusting successfully. The loss of gibbons has been low throughout the 10-year period and only five have been lost to unknown fates (Table 2).

The released gibbons that have remained in the wild have, through new births, expanded their population to 23 individuals by the end of 2012. Eleven infants have been born in the wild to five females. There have been nine live births, of which one infant died after just one week and a second disappeared shortly after his second birthday. Seven wild-born gibbons remain alive at the time of writing, the oldest of which has already reproduced. The two young females (one released as a juvenile, the other wild-born) that have matured, dispersed and reproduced have given birth to their first babies at 9 years 7 months and 9 years 11 months, respectively. Three females have given birth more than once to infants that survived to at least two years. The interbirth-intervals between these infants averaged 38.5 months (N = 4; intervals = 33, 35, 38 and 48 months; SD = 6.7) (Table 3).

**Table 1.** The percentage of reintroduced, captive raised, individuals from each family that remain within the reintroduction site, 1–10 years after their release.

| Release year | No individuals released | %1 year | %2 years | %5 years | %10 years |
|---|---|---|---|---|---|
| 2002 | 3 | 100 | 100 | 100 | 66 |
| 2003 | 4 | 100 | 75 | 75 | |
| 2004 | 4 | 75 | 25 | 25 | |
| 2006 | 3 | 0 | | | |
| 2006 | 2 | 50 | 50 | 50 | |
| 2007 | 4 | 100 | 50 | 50 | |
| 2009 | 3 | 100 | 66 | | |
| 2011 | 4 | 75 | | | |
| 2012 | 3 | | | | |

After her second release in 2011, the adult female Kushta has had two miscarriages or stillbirths in the forest. The first infant was observed dead during the family's initial months in the wild when the female was being claimed by a "wild" male (Arun, released as a 1-year-old infant in 2003), who expressed what appeared to be infanticidal behaviour toward the newborn infant. The subadult father of Kushta's infant did not defend his offspring, and had immediately exhibited submissive behaviours towards Arun. The dead infant's body was never recovered after the mother was seen carrying it around one day and infanticide could never be definitely confirmed. However, shortly after this incident Kushta's nearly 3-year-old juvenile daughter from a previous pairing was also attacked by the male and eventually she had to be separated from her family and returned to captivity**.** Arun has since stayed with Kushta and the rest of her family.

Wild-born infant mortality (stillbirth or death in the first months of life) in the reintroduced population was 18%, not including the death of Kushta's first infant, since she was not living in a natural group situation at the time and her situation was further complicated by release stress and a group takeover by the infanticidal male.

With the exception of Kushta's first family, at least one individual from each reintroduction attempt remains in the wild today. Members of all the other reintroduced families have managed to adapt, either as a unit or by joining already existing groups. This social flexibility means that four out of the current six groups are, or were at some point, non-nuclear families, consisting of merged groups or containing "adopted" juveniles, as identified in the group summaries above.

## Discussion

The white-handed gibbon is the most common gibbon species in zoos around the world. Despite its apparent abundance, the species has experienced a severe (more than 50%) decline in numbers in the past 40 years and is listed as Endangered on IUCN's Red List (Brockelman and Geissmann 2008). In 1975, Brockelman (1975) estimated that forests in Thailand could harbor as many as 220,000 white-handed gibbons, but by 1990 the maximum number was estimated at 110,000 (Tunhikorn *et al.* 1993; Tilson *et al.* 1997) and declining rapidly. These declines have been due mostly to hunting rather than to deforestation (Brockelman 1993–1994), so the population cannot simply be estimated by extrapolation over the forests in the protected area system without intensive sampling. There is no recent estimate of the current population in

**Table 2.** Details of the reintroduced gibbons and their fates to date.

| | Name | Sex | Date of birth | Place of birth | Back-ground | Date of rescue | Years at GRP | Age at release | Date of release | Result | Status December 2012 | Comments |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | Kip | F | 1989 | Wild | Pet trade | 09/05/1994 | 8+ | 13 | 05/10/2002 | Wild | Wild | |
| 2 | Joe | M | 1985 | Wild | Pet trade | 09/05/1994 | 8+ | 17 | 05/10/2002 | Wild | Wild | |
| 3 | Thong | M | 19/02/2000 | GRP | GRP | na | 2,5 | 2,5 | 05/10/2002 | Wild/translocated | wild | |
| 4 | Lek | F | 1992 | Wild | Pet trade | 06/02/1994 | 9+ | 11 | 15/08/2003 | Wild | Wild | Pair with Bank 2006 |
| 5 | Bo | M | 1987 | Wild | Pet trade | 27/10/1993 | 10 | 16 | 15/08/2003 | Returned | GRP | Voluntary return |
| 6 | Dao | F | 08/05/2000 | GRP | GRP | na | 3+ | 3+ | 15/08/2003 | Wild | Wild | Pair with Payu 2008 |
| 7 | Arun | M | 02/09/2002 | GRP | GRP | na | 1 | 1 | 15/08/2003 | Wild | Wild | Pair with Kushta 2011 |
| 8 | Pompam | F | 1989 | Wild | Pet trade | 13/07/1995 | 9 | 15 | 10/12/2004 | Poached 2006 | Dead | |
| 9 | Bird | M | 1988 | Wild | Pet trade | 13/07/1995 | 9 | 16 | 10/12/2004 | Disappeared | na | Disappeared after fights with Joe and Bo in 2005 |
| 10 | Sabai | F | 01/02/2000 | GRP | GRP | na | 5- | 5- | 10/12/2004 | Returned | Dead | Returned with injuries from attack by Lek in 2006, died of pneumonia at GRP 2008 |
| 11 | Yoge | M | 21/06/2003 | GRP | GRP | na | 1,5 | 1,5 | 10/12/2004 | Wild | Wild | Pair with Hope 2011, 1st wild-born to Kip |
| 12 | Bank | M | 2000 | Wild | Semi wild | 21/11/2005 | <0,5 | 6 | 07/02/2006 | Wild | Wild | Pair with Lek 2006 |
| 13 | Khun Nguan | M | 2000 | Wild | Semi wild | 21/11/2005 | <0,5 | 6 | 07/02/2006 | Returned | dead | Returned to GRP with medical complications in 2006, died. |
| 14 | Kushta | F | 1990 | Wild | Photo prop | 06/04/1996 | 10 | 16 | 10/03/2006 | Returned | wild | Re-release in 2011 |
| 15 | Bozo | M | 1989 | Wild | Pet trade | 28/05/1993 | 13 | 17 | 10/03/2006 | Disappeared | na | |
| 16 | Nat | M | 19/09/2004 | GRP | GRP | na | 1,5 | 1,5 | 10/03/2006 | Returned | Wild | Re-release in 2011 |
| 17 | Nuan | F | 1986 | Wild | Pet trade | 22/09/1996 | 11 | 21 | 26/09/2007 | Returned | GRP | Returned with injuries after fight with Dao in 2008 |
| 18 | Khao | M | 1991 | Wild | Pet trade | 18/11/1995 | 12 | 16 | 26/09/2007 | Poached 2008 | Dead | |
| 19 | Payu | M | 14/07/2001 | GRP | GRP | na | 7- | 7- | 26/09/2007 | Wild | Wild | Pair with Dao in 2008 |
| 20 | Namthip | F | 18/03/2006 | GRP | GRP | na | 1,5 | 1,5 | 26/09/2007 | Wild | Wild | |
| 21 | Jita | F | 1993 | Wild | Photo prop | 07/06/1994 | 15 | 16 | 10/12/2009 | Disappeared | na | |
| 22 | Tony | M | 1991 | Wild | Photo prop | 07/06/1994 | 15 | 18 | 10/12/2009 | Returned | GRP | Recaptured due to aggressive behavior towards humans 2012 |
| 23 | Claire | F | 26/11/2008 | GRP | GRP | na | 1 | 1 | 10/12/2009 | Wild | Wild | Adopted by Hope & Yoge 2012 |
| 24 | Kushta | F | 1990 | Wild | Photo prop | 06/04/1996 | 15 | 21 | 27/04/2011 | Wild | Wild | Pair with Arun 2011 |
| 25 | Muki | M | 2004 | Wild | Photo prop | 03/01/2006 | 5 | 7 | 27/04/2011 | Wild | Wild | |
| 26 | Nat | M | 19/09/2004 | GRP | GRP | na | 6.5 | 6,5 | 27/04/2011 | Wild | Wild | |
| 27 | Pee Mai | F | 01/01/2009 | GRP | GRP | na | 2+ | 2+ | 27/04/2011 | Returned | GRP | Recaptured 2012 after being attacked by Arun |
| 28 | Cop | F | 2002 | Wild | Photo prop | 04/03/2004 | 8+ | 10 | 18/11/2012 | Wild | Wild | |
| 29 | Jorn | M | 2004 | Wild | Pet trade | 18/05/2006 | 6+ | 8 | 18/11/2012 | Wild | Wild | |
| 30 | Sherpa | M | 03/10/2010 | GRP | GRP | na | 2 | 2 | 18/11/2012 | Wild | Wild | |

Thailand, or the world. The unknown rates of current decline make it imperative to develop diverse approaches to conservation that involve management and protection of both wild and captive populations.

Past gibbon translocations have received a lot of criticism due to inadequate planning and post-release monitoring, poor survival, and the fact that these efforts have been so poorly shared and published (Loftin 1995; Ware 2001; Cheyne 2009b). We wish to help rectify this problem by describing in detail the dynamics of the reintroduced population in the longest running gibbon reintroduction program in the world.

The first gibbon family released by the GRP in 2002, using the described soft release method, has fulfilled the three criteria for successful reintroduction listed by Cheyne (2009b): they have survived 10 years post-release; they have maintained the original pair bond; and they have reproduced in the wild, in this case raised three wild-born babies past infancy. Eleven gibbons have been wild-born at the reintroduction site, including a second-generation infant to the first wild-born female of this first family.

We have reached the point at which reintroduction of gibbons seems feasible, although it does require considerable labor and cooperation among diverse stakeholders to succeed. At the GRP, 83% of animals participating in the reintroductions have survived the process, 60% of reintroduced animals have adapted, or appear to be adjusting, to life in the wild, and 53% of all gibbons reintroduced during the past 10 years are still living at the original reintroduction site. This is comparable with the 57% survival of wild-born golden lion tamarins participating in the often-cited successful population restoration project (Beck 1995). Of the zoo-born tamarins only 27% survived their release. Recent translocations of great apes have also achieved good survival rates. In the conservation translocation attempt of 51 western gorillas in Congo and Gabon between 1996 and 2006, survival was 84% (King and Courage 2008) and of 37 released chimpanzees in the Congo, 62% still remained in the release area after eight years, whilst some of the females that had disappeared were believed to be alive having joined wild groups (Goossens *et al.* 2005). The high survival rate of the chimpanzees was partially attributed to medical intervention. At the GRP, the 83% survival rate may likewise be due in part to long-term human assistance and medical intervention. In comparison, only about 65% of the gibbons available to the GRP were deemed fit enough to attempt reintroduction at all, which indicates that no more than 40% of gibbons received by GRP have been, or may be, successfully reintroduced.

That gibbons may be more flexible in lifestyle and behavior than often given credit for (Palombit 1994, 1996; Reichard and Sommer 1997; Brockelman *et al.* 1998; Fuentes 2000; Whittaker and Lappan 2009) raises hopes for their adaptability under artificial conditions. Long-term data from

**Table 3.** Reproductive females in KPT, their ages at first births and interbirth intervals.

| Female | Origin | Age at first birth | Name and gender of offspring | Offspring's D.O.B | Offspring's place of birth | Interbirth interval* |
|---|---|---|---|---|---|---|
| KIP[1] | Pet trade | ~6–7yrs | Tara (f) | 19-Dec-95 | GRP | Firstborn |
| | 1989 | | Bamboo (m) | 03-Jan-98 | GRP | 24,5 |
| | | | Thong (m) | 19-Feb-00 | GRP | 24,5 |
| | | | Hope (f) [1] | 21-Oct-02 | Wild in KPT | 32 |
| | | | Toffee (f) [1] | 21-Oct-06 | Wild in KPT | 48[2] |
| | | | Omyim (f) [1] | 30-Dec-09 | Wild in KPT | 38[2] |
| LEK[1] | Pet trade | ~8yrs | Dao (f) [1] | 08-May-00 | GRP | Firstborn |
| | 1992 | | Arun (m) [1] | 02-Sep-02 | GRP | 28 |
| | | | Kopi (?)[4] | 20-Nov-07 | Wild in KPT | 60,5 |
| | | | Redy (m) [5] | 25-Sep-08 | Wild in KPT | 10 |
| | | | Peanut (m) [1] | 30-Jun-11 | Wild in KPT | 33[2] |
| DAO[1] | GRP, | 9yrs, 7months | Newbe-Mek(m) [1] | 20-Dec-09 | Wild in KPT | Firstborn |
| | May-00 | | | | | |
| | | | Sai Fa (?)[1] | 01-Nov-12 | Wild in KPT | 35[2] |
| KUSHTA[1] | Tourism | ~10 yrs | Yindee (f) | 2000 | GRP | Firstborn |
| | 1990 | | ? [3] | 2003 | GRP | 36 |
| | | | Nat (m) [1] | 19-Sep-04 | GRP | 12 |
| | | | Pee Mai (f) | 01-Jan-09 | GRP | 52 |
| | | | ? [3] | 06-Jul-11 | Wild in KPT | 30 |
| | | | ? [3] | 05-Apr-12 | Wild in KPT | 9 |
| HOPE[1] | Wild in KPT | 9yrs, 11months | Happy (?)[1] | 01-Sep-12 | Wild in KPT | Firstborn |
| | Oct-02 | | | | | |

*Months since previous infant. [1]Gibbons surviving in KPT at time of writing, [2]individuals used in calculating the interbirth interval between surviving wild born infants, [3]Stillborn or dead after birth, [4]Died after one week, [5]Died after two years.

Ketambe in Sumatra (Palombit 1994, 1996) and Khao Yai National Park in Thailand, has raised doubts on the traditional belief that gibbons are obligatorily monogamous and strictly territorial (Reichard and Sommer 1997; Brockelman et al. 1998; Sommer and Reichard 2000; Bartlett 2003; Reichard and Barelli 2008). In an 18-year-long study in Khao Yai Nationl Park, only two-thirds of the 13 study groups showed social monogamy, and none of the groups exhibited life-long monogamy. Some groups showed considerable territorial overlap where, often friendly, interactions with neighbors, known to be relatives, occurred (Reichard and Sommer 1997; Sommer and Reichard 2000; Bartlett 2003). Gibbon groups in KPT have also proved to be socially flexible, and four of the current six family groups are, or have at some point been, non-nuclear, consisting of merged groups or containing "adopted" juveniles. A similarly interesting observation on gibbon social flexibility was also noted from the SMRL project in 1976 and 1977 when four released gibbons joined wild gibbon groups in the release area (Tingpalapong *et al.* 1981).

The life history characteristics of gibbons released in KPT have also been shown to be similar to those of wild gibbons. The interbirth interval for the three females that gave birth more than once in the wild averaged 38.5 months between surviving infants, comparable to the average (41 months) for wild white-handed gibbons in Kao Yai Park (Brockelman *et al*. 1998; Reichard and Barelli, 2008). The age at first birth for two young females, one wild born herself and the other reintroduced as a juvenile, was just below 10 years, also within the range of wild gibbons in Khao Yai (usually 9–12 years; Brockelman *et al.* 1998; Reichard and Barelli 2008).

The results at GRP give some hope with regard to the possibility of using reintroduction as a management method for captive gibbons in the future. It remains uncertain whether reintroduction of long-lived primates will ever play a significant role in the conservation of the species or just serve the more modest goal of restoring local ecosystem function where gibbons used to play important roles as seed dispersers (Osterberg *et al.* in press).

In Thailand, as in other habitat countries, long-term management of gibbon species in captivity is not an option. Even if the many gibbons in captivity were made available, developing a sustainable captive population, as is being implemented in North American and European zoos for some species, would be prohibitively expensive. The Thai government's Wildlife Conservation Division devotes nearly all its resources to conserving wild populations and habitats, and has no programs besides the GRP for either captive breeding or translocation of gibbons. The care of the captive population is justified only in terms of promoting animal welfare—particularly for the endless stream of confiscated and donated individuals arriving from the illegal wildlife trade. In all habitat countries, this mindset is likely to change only if—or when—the populations decline to critical levels.

The educational programs developed by GRP have been strongly beneficial to the project. They change peoples' attitudes to zoos and captive animals in general. The thinking is guided toward conservation problems of the population, and the project clearly makes the connection between captive gibbons and what is happening in the wild. The message is one of compassion towards the population, with the aim of inspiring people to value the conservation of the species in the wild, and making people see that being placed in a cage, or on the end of a chain, is traumatic for a gibbon. As such, the GRP hopes to inspire a wider motivation to participate in and support the reintroduction program.

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# Geza Teleki (1943–2014)

Geza Teleki in Sierra Leone in 1984. Photo courtesy of Heather McGiffin.

Born in Hungary, Geza Teleki emigrated to the United States with his family at the age of six. At the end of a career devoted mainly to the study of chimpanzees, when the onset of multiple organ failures began to seriously affect his quality of life, he returned to Hungary, where he died on Szentendre Island on January 7, 2014. He is survived by his wife, Heather McGiffin, and their son, Aidan.

Geza's involvement with chimpanzees began in 1968, when he persuaded Louis Leakey to send him to work with Jane Goodall, then in the beginning phases of her lifelong study of the chimpanzees of the Gombe Stream Reserve in Tanzania. After two years he returned to study primatology with C. Ray Carpenter at Pennsylvania State University. In 1973 he published "Predatory Behavior in Wild Chimpanzees," and in the following years he was a co-editor of "Omnivorous Primates: Gathering and Hunting in Human Evolution."

In the late 1970s, Geza's attention was drawn to Sierra Leone in West Africa, where numbers of applications to export chimpanzees were greater than the estimated population could have sustained. As a result, with World Wildlife Fund support he and Lori Baldwin carried out the first population survey of chimpanzees in Sierra Leone in 1979–1980. This survey convinced Geza that the most important site for chimpanzee conservation in that country was in the Outamba and Kilimi regions in the northwest. He persuaded the World Wildlife Fund to support a proposal to create an Outamba-Kilimi National Park (OKNP) and spent the early 1980s in Sierra Leone directing efforts to establish the park. Practical difficulties and a lack of funds delayed full gazettement of the park until 1995, but OKNP still protects the largest chimpanzee population in Sierra Leone and stands as a lasting testament to Geza's efforts.

Returning to the United States in 1984, Geza concentrated on chimpanzee conservation. His efforts helped to prevent the establishment of a medical research station in Sierra Leone that would use captive chimpanzees. In 1986 he was among the founders of the Committee for the Conservation and Care of Chimpanzees, and later became its chairman. He continued to do free-lance conservation work for the World Wildlife Fund and to make other significant contributions to improve the lot of both wild and captive chimpanzees.

Geza was a man of high intelligence with great persuasive abilities. He had a creative imagination, and was never daunted by tasks of great complexity, such as the Outamba-Kilimi National Park. Persistence and determination were characteristic of all his endeavors. Geza had a somewhat skeptical opinion of *Homo sapiens* in the aggregate, although he had admiration for and warm friendships with many different individuals. He thought much more highly of chimpanzees as a species, in fact, and it was this view that motivated his many successful efforts on their behalf.

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*University of Pennsylvania, Philadelphia, PA*

*See also:*
<http://www.anatomyofabeast.com/Blog/9ECE6649-7417-4431-A161-4A9E8FCF97B2.html>
<http://www.anatomyofabeast.com/Blog/FC274A8D-23FE-45C0-BED1-6FB9F1DE1D8E.html>
<http://www.animal-rights-library.com/texts-m/teleki01.htm>

*Primate Conservation* 2014 (28): 191–192

# Pius A. Anadu (1940−2014)

Pius instructing students on the processing of small mammal specimens in the course of a survey, sponsored by WCS, on the Obudu Plateau, Nigeria. 2005. Photo by Andrew Dunn.

Pius Anadu died in London on 11 December 2014, at the age of 74. Pius was the first Nigerian member of the Primate Specialist Group and during a distinguished career played a leading role in primatology, mammalogy and wildlife conservation in Nigeria. He participated in surveys in the 1980s that led to the re-discovery of wild populations of white-throated monkeys (*Cercopithecus erythrogaster*) and Sclater's monkeys (*Cercopithecus sclateri*), two little-known species that had been feared to be possibly extinct; and he helped to establish the Okomu Wildlife Sanctuary (now National Park), a key conservation area for the white-throated monkey and other threatened species, including red-capped mangabeys.

Pius was born on 11 November 1940 in Nnewi, in what is now Anambra State, in eastern Nigeria. He grew up in a large, loving family with numerous sisters and brothers, cousins, nieces and nephews. He won a scholarship to study zoology at University College Ibadan (now the University of Ibadan), graduating with a B.Sc. in 1964. His subsequent career was interrupted by the Nigerian civil war. Not long before the outbreak of war in 1967 he re-located to the University of Nigeria, Nsukka, in what was soon to become Biafra. After the conflict began Pius enlisted as an officer in the Biafran army, and was subsequently wounded in the fighting.

When the civil war ended in 1970, Pius returned to Ibadan, and, in 1973, completed his doctoral thesis on the ecology and breeding biology of small mammals under the supervision of Dr. David Happold. The data from some of the papers that Pius published based on this research were used for species profiles in the *Mammals of Africa* (2013), a testimony to the lasting value of his work.

In 1979, Pius transferred from Ibadan to the University of Benin, where he was initially a senior lecturer in Zoology and eventually the Acting Head of the Department for Forestry and Wildlife. Increasingly he dedicated himself to the conservation of endangered species and to the protection of the environment in Nigeria, and was one of the first to draw attention to the impact of the commercial bushmeat trade on African forest wildlife. In 1988, he was appointed Executive Director of the Nigerian Conservation Foundation in Lagos and built an international reputation for both himself and the foundation; in 1992, under Pius's leadership, NCF won a UNEP Global 500 Roll of Honour award. After leaving NCF in 1994, Pius worked with the British Council in Lagos as an Assistant Director, where he was responsible for the council's program in the environment and renewable natural resources.

In his later years Pius became a consultant in environmental impact assessment. Among several projects he worked on in West Africa was a mission to Sierra Leone, where he assessed poorly-known small mammal populations in the Loma Mountains and Gola Forest, prior to these two important conservation areas being gazetted as national parks. After his retirement he moved to London, where his wife Christine (his college sweetheart) was working with the National Health Service.

Pius Anadu was a most knowledgeable, thoughtful, tolerant and modest man, who always spoke with care and grace. He was devoted to his family, and he and Christine raised two daughters (Ijeoma and Chinwe) and two sons (Obinna and Emeka), all of whom have gone on to establish successful careers.

*John F. Oates*
*16 January 2015*

Some of Pius Anadu's papers on Nigerian primates and on conservation:

Oates J. F. and P. A. Anadu. 1982. Report on a survey of rainforest primates in southwest Nigeria. *Primate Conservation* (2): 17.

Anadu, P. A. 1987. Prospects for conservation of forest primates in Nigeria. *Primate Conservation* (8): 154–159.

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# Regional Newsletters

The IUCN SSC Primate Specialist Group also produces regional newsletters/journals which publish short articles and notes on general and specific aspects of primate ecology, taxonomy, distributions, behavior and conservation, tropical forest ecology and conservation, forest destruction, and protected areas. Also please send information on projects, research groups, events, recent publications, courses, funding sources, activities of primatological societies and NGOs, and other newsworthy items of interest to primate conservationists, directly to the editors at the addresses below.

**Madagascar** - *Lemur News*

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**Neotropical Region** - *Neotropical Primates,* Mesoamerica

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**Neotropical Region** - *Neotropical Primates,* South America

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**Asian Region** - *Asian Primates Journal*

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**African Region** - *African Primates*

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The four newsletters and *Primate Conservation* are available, open access, at <http://www.primate-sg.org/journals_and_newsletters/>.

# Instructions to Contributors

**Articles submitted to *Primate Conservation***

*Manuscript Format*
All manuscripts should be type written, double spaced, with generous margins, and submitted electronically as a Word document or in Rich Text Format (rtf). Please indicate on a separate cover page the corresponding author, address, and e-mail, the date of submission, up to six key words, and a short running title. Please provide an abstract of 300–500 words. Footnotes are to be avoided (except in tables and figures). IMRAD subtitles can be used but are not obligatory. Please give all measurements in metric units. Please take special care concerning diacritical marks of languages other than English. Bibliographic references should be in the following style:

Example – journal article:
Struhsaker, T. T. 1972. Rain-forest conservation in Africa. *Primates* 13: 103–109.

Example – chapter in book:
Goodall, A. G. and C. P. Groves. 1977. The conservation of eastern gorillas. In: *Primate Conservation*, H. S. H. Prince Rainier of Monaco and G. H. Bourne (eds.), pp.599–637. Academic Press, New York.

Example – book:
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Example – dissertation:
Homewood, K. M. 1976. Ecology and Behaviour of the Tana Mangabey (*Cercocebus galeritus galeritus*). PhD thesis, University College, London.

Example – Website:
Nijman, V. and Supriatna, J. 2008. *Trachypithecus auratus*. In: IUCN 2009. *IUCN Red List of Threatened Species*. Version 2009.2. Website: <http://www.iucnredlist.org/>. Downloaded 11 December 2012.

*Maps*
Maps should always be made as concise as possible and should include an inset showing the location of the area discussed in relation to its home country or continent.

*Photographs and Figures*
Please indicate on all figures the title and author of the manuscript to which they belong and package them carefully to avoid damage in the post. Figures will only be returned at the special request of the author. Electronic high resolution files (300 dpi) of maps, photographs and figures can be sent in any one of the following types of files: EPS, TIF, or JPG. Please, however supply a hard copy of all drawn maps or figures, preferably in the size in which they should be published.

We are always interested in receiving high quality photographs for our covers, especially images of little known and rarely photographed primates, even if they do not accompany an article.

*Please send your contribution to:*

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**Back cover:** The crowned sifaka, *Pithecia coronatus*, is one of 106 lemur taxa endemic to Madagascar, over 90% of which are threatened with extinction. This issue of *Primate Conservation* highlights the current knowledge and conservation needs of the crowned sifaka across its highly fragmented distribution. Katsepy, Madagascar, July 2010. Photo by Tony King / The Aspinall Foundation.