

Extensive survey of the Endangered Coquerel's sifaka *Propithecus coquereli*

Jordi Salmona^{1,*}, Fabien Jan¹, Emmanuel Rasolondraibe², Aubin Besolo²,
Dhurham Saïd Ousseni², Angelika Beck¹, Radavison Zaranaina²,
Heriniaina Rakotoarisoa², Clément Joseph Rabarivola², Lounès Chikhi^{1,3,4}

¹Instituto Gulbenkian de Ciência, Rua da Quinta Grande, 6, 2780-156 Oeiras, Portugal

²Faculté des Sciences, Université de Mahajanga, BP 652 401 Mahajanga, Madagascar

³CNRS, Université Paul Sabatier, ENFA; UMR 5174 EDB (Laboratoire Evolution & Diversité Biologique), 118 route de Narbonne, 31062 Toulouse, France

⁴Université de Toulouse; UMR 5174 EDB, 31062 Toulouse, France

ABSTRACT: Coquerel's sifaka *Propithecus coquereli* has a large but highly fragmented distribution. Despite its Endangered (EN) IUCN conservation status, uncertainties persist regarding its actual distribution and its presence in forests that are thought to be part of its distribution range. We provide here the first extensive population surveys of Coquerel's sifaka across a large number of forest fragments neighboring 27 sites of its known and expected distribution range in north-western Madagascar, including 12 previously visited sites. During our diurnal surveys carried out in the dry seasons from 2009 to 2011 we observed the species in 26 of the 27 visited sites. Combining our results with previously published data, we propose a refined update of the species' distribution range and identify areas to be surveyed. We also recorded the support tree species on which sifakas were observed, and note that, surprisingly, *P. coquereli* was frequently seen around villages and in areas dominated by introduced tree species. Although the species was present at almost all the visited sites of its highly fragmented distribution range, it remains unclear how viable the populations of a significant proportion of these sites actually are. Due to political instability and high rates of deforestation, large-scale conservation actions are urgently needed. We thus (1) discuss the outline of a possible metapopulation conservation action plan for *P. coquereli* and (2) identify priority sites and actions.

KEY WORDS: Survey · Distribution range · *Propithecus coquereli* · Sifaka · Lemur · Madagascar

— Resale or republication not permitted without written consent of the publisher —

INTRODUCTION

In the last couple of decades our knowledge of the distribution and number of lemur species across Madagascar has increased (Mittermeier et al. 2008, 2010, Schwitzer et al. 2013). However, there is still no baseline data (i.e. distribution, abundance) available for many regions and species, including recently discovered species (Weisrock et al. 2010). For species that have been known for decades but are distributed over a wide area or live in little-studied regions, data may be similarly deficient (Ravaloharimanitra et al. 2011, Rakotonirina et al. 2013, Salmona et al. in press).

This is the case for Coquerel's sifaka *Propithecus coquereli*, which was historically reported to inhabit the Sofia region between the Betsiboka and Maevarano watersheds (Mittermeier et al. 2010, Wilmé et al. 2012; Fig. 1). The distributions typically reported for many lemurs, including *P. coquereli*, are based on a relatively limited number of actual observations in the field. Despite the Endangered (EN) status (IUCN 2013, Schwitzer et al. 2013) of the Coquerel's sifaka and its possible role as an umbrella species for the conservation of other species, regions or habitats, no extensive survey of its whole distribution range has ever been conducted. The last meeting of the IUCN Species Survival Commission (SSC) for lemur Red

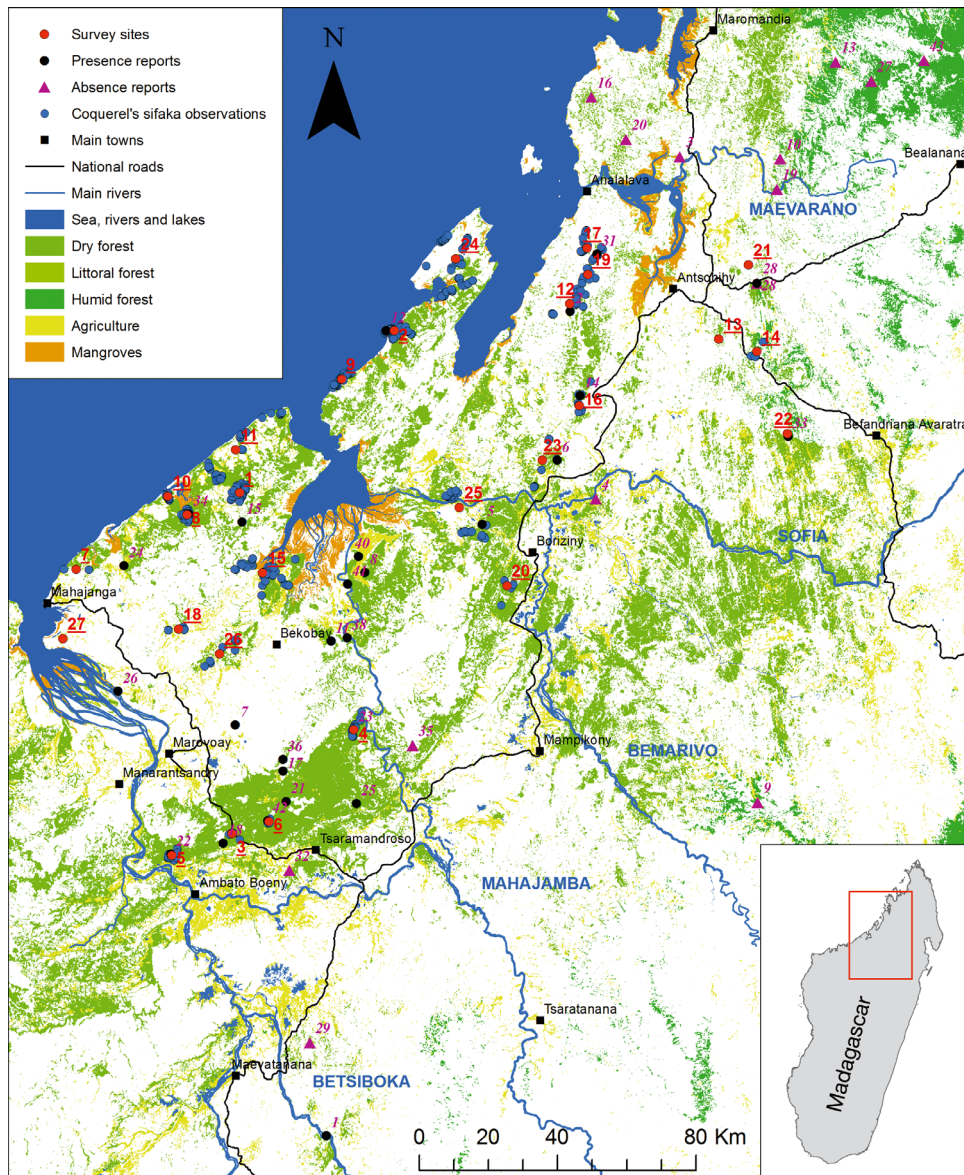


Fig. 1. Surveyed sites and *Propithecus coquereli* presence/absence bibliographic report locations in NW Madagascar. Purple italic numbers refer to reports and correspond to location numbers in Table 1; red underlined numbers refer to surveyed sites or forests and correspond to the location numbers in Table 2. Vegetation areas are taken from Moat & Smith (2007)

List reassessment in 2012 led to the proposal of only 3 conservation priority sites within the known distribution range of *P. coquereli* (Schwitzer et al. 2013, 2014). Nevertheless, a species with such a large and highly fragmented distribution range should be conserved using a metapopulation management strategy, as suggested for its sister species *P. coronatus* (King et al. 2012). To develop this type of approach, and identify priority areas suitable for local management/conservation projects, a good knowledge of the existing populations and of their distribution range is required. In this context, and considering the rapid

forest loss and fragmentation across western Madagascar (MEFT, USAID, CI 2009), we conducted this urgently needed survey.

MATERIALS AND METHODS

We surveyed 26 sites in northwestern Madagascar, including 12 that had previously been surveyed (Tables 1 & 2, Fig. 1). Sites were chosen based on (1) previous bibliographic presence reports of *Propithecus coquereli* (Table 1), (2) vegetation maps and atlas

Table 1. Bibliographic review of *Propithecus coquereli* reports. Site numbers refer to the presence or absence of the species at the (purple italic) location numbers in Fig. 1

Site	Site no.	GPS (°S)	GPS (°E)	Year	Period	Presence/Absence	Reference
Ambalanjanakomby	1	17.10	47.08	2010	Oct	Presence	Rakotonirina et al. (in press)
Ambarijeby	2	14.94	47.71	2004	May to Jun	Presence	Olivieri et al. (2005)
Ambendrana	3	14.53	48.00	2003	Jul to Sep	Absence	Randriatahina & Rabarivola (2004)
Ambodimadiro, Sofia ^a	4	15.43	47.79	2004		Absence	G. Rakotoarisoa (pers. comm.)
Ambodimadiro, Maevarano	43	14.27	48.65	2003	July to Sep	Absence	Randriatahina & Rabarivola (2004)
Ambodimahabibo	5	15.50	47.48	2004	Jul to Aug	Presence	Olivieri et al. (2005)
Ambongabe	6	15.33	47.68	2003	Jul to Aug	Presence	Olivieri et al. (2005)
Ampijoroa, Ankarafantsika	7	16.03	46.82	1962		Presence	Petter (1962)
		16.03	46.82	1974		Presence	Richard (1974)
		16.03	46.82	1978		Presence	Richard (1978b)
		16.03	46.82	1981		Presence	Albignac (1981)
		16.03	46.82	1985 & 1986	Dec & Jan	Presence	Ganzhorn (1988)
		16.03	46.82	2000	Sep	Presence	Radespiel & Raveloson (2001)
		16.03	46.82	2007 to 2008		Presence	McGoogan (2011)
		16.03	46.82	2009	Jul to Aug	Presence	Kun-Rodrigues et al. (2014)
		16.30	46.82	1969 to 1974		Presence	Sussman (1977)
Analalabe ^a	8	15.63	47.17	2004		Presence	G. Rakotoarisoa (pers. comm.)
Analamaitso, Tampoketsa BB	9	16.22	48.23	1999	Jul	Absence	Ralison (2000)
Andakalaka ^a	26	16.95	46.50	2009		Presence	S. Wohlhauser (pers. comm.)
Andranobe	10	14.54	48.27	2003	Jul to Sept	Absence	Randriatahina & Rabarivola (2004)
Andranolava, Lac	11	15.81	47.08	1997	May to Jul	Presence	Wilmé et al. (2006)
Anjajavy, Ankidivy	12	15.00	47.22	2004	Jul	Presence	Wilmé et al. (2006)
Anjajavy, Hôtel & S		15.00	47.23	2004	Jul	Presence	Wilmé et al. (2006)
Anjajavy, near Grotte Unique		15.05	47.24	2004	Jul	Presence	Wilmé et al. (2006)
Anjavidimarina	13	14.28	48.41	2003	Jul to Sep	Absence	Randriatahina & Rabarivola (2004)
Anjamangirana I	14	15.16	47.74	2004	Sep to Oct	Presence	Olivieri et al. (2005)
Anjohibe, Grottes d'	15	15.50	46.83	1962	Oct	Presence	Wilmé et al. (2006)
Ankarafa	16	14.38	47.76	2004	Oct	Absence	Olivieri et al. (2005)
		14.38	47.76	2003	Jul to Sept	Absence	Randriatahina & Rabarivola (2004)
Ankarafantsika	17	16.15	46.95	1959	Oct	Presence	Wilmé et al. (2006)
Ankarokaroka, Ankarafantsika	18	16.34	46.79	1997	Feb	Presence	Schmid & Rasoloarison (2002)
		16.34	46.79	2000	Sep	Presence	Radespiel & Raveloson (2001)
Ankiabe	19	14.61	48.26	2003	July to Sep	Absence	Randriatahina & Rabarivola (2004)
Antsakoamamy	20	14.49	47.85	2003	Jul to Sep	Absence	Randriatahina & Rabarivola (2004)
Antsiloky, Ankarafantsika	21	16.23	46.96	1997	Feb	Presence	Schmid & Rasoloarison (2002)
Bealana, Ankarafantsika	22	16.37	46.65	2009	Aug to Sep	Presence	Kun-Rodrigues et al. (2014)
Beronono, Ankarafantsika	23	16.04	47.14	2009	Aug	Presence	Kun-Rodrigues et al. (2014)
Betsaka	24	15.62	46.52	1891	Jan	Presence	Wilmé et al. (2006)
Bevazaha, Ankarafantsika	25	16.23	47.15	1950	Feb	Presence	Wilmé et al. (2006)
		16.23	47.15	2000	Sept	Presence	Radespiel & Raveloson (2001)
Bongomarina	27	14.33	48.51	2003	July to Sept	Absence	Randriatahina & Rabarivola (2004)
Bora	28	14.86	48.21	2004	Jun	Presence	Olivieri et al. (2005)
		14.86	48.21	2005	Dec	Absence	Koenig & Zavasoa (2006)
		14.87	48.20	2002	May to Jun	Presence	Randrianambinina et al. (2003)
Le Croisement	29	16.86	47.03	2003	May	Absence	Olivieri et al. (2005)
Mahajamba complex	12	15.03	47.27	2007	July	Presence	Ravoahangy et al. (2008)
Mahatsinjo	31	14.79	47.78	2004	Sep	Presence	Olivieri et al. (2005)
Mangatelo	32	16.41	46.97	2003	May to Jun	Absence	Olivieri et al. (2005)
Marasakoa	33	15.26	48.30	2004	Jul	Presence	Olivieri et al. (2005)
Mariarano	34	15.48	46.69	2003	Jul	Presence	Olivieri et al. (2005)
		15.48	46.69	2006	Nov	Presence	Rambintinsoa et al. (2006)
Maroakata	35	16.08	47.30	2003	Aug to Sep	Absence	Olivieri et al. (2005)
Ste Marie	36	16.12	46.95	2000	Sep	Presence	Radespiel & Raveloson (2001)
Tananvaovao	34	15.47	46.67	2003	Jul to Aug	Presence	Olivieri et al. (2005)
Tsiaramaso	38	15.80	47.12	2003	Oct	Presence	Olivieri et al. (2005)
Tsimaloto, Ankarafantsika	25	16.23	47.14	1997	Feb	Presence	Schmid & Rasoloarison (2002)
Tsinjoarivo ^a	40	15.59	47.15	2004		Presence	G. Rakotoarisoa (pers. comm.)
Tsinjomitondraka	41	15.66	47.12	2004	Aug	Presence	Olivieri et al. (2005)
Vava'ny Marovoay	42	16.28	46.91	2009	Aug	Presence	Kun-Rodrigues et al. (2014)

^adenotes newly reported sites (not previously published)

Table 2. Survey details. This table lists the surveyed sites and effort information, *Propithecus coquereli* presence and relative encounter frequencies. Site numbers refer to surveyed sites and correspond to the red underlined location numbers in Fig. 1; site names are those of the closest village or chief town. Sites are sorted by year of survey and alphabetically. Number of people involved only takes trained field researchers into account. Group size range represents the minimum and maximum group size observed

Site no.	Site	Region	Commune	GPS NS	GPS EW	Year	Period	a: Days of survey (n)	People involved (n)	b: Independent teams (n)	c: Survey effort: (a × b)	d: Observed groups (n)	Observed ind. (n)	Observed newborns (n)	Group encounter frequency (d/c)	Group size range	Groups on local tree species (n)	Groups on introduced tree species (n)	Groups on introduced tree species (%)
1	Analabe-Antanambao	Boeny	Mariarano	-15.424	46.826	2009	Jul	3	3	2	9	33	113	9	3.7	1-6	23	2	8
2	Anjaviy	Sofia	Antonibe	-14.996	47.239	2009	Oct	3	5	4	15	47	165	18	3.1	1-9	29	2	6
3	Ampijoroa	Boeny	Andranofasika	-16.315	46.814	2009	Aug	5	3	3	15	6	23	1	0.4	1-5	2	0	0
4	Beronono	Boeny	Ankazomborona	-16.040	47.141	2009	Aug	3	3	3	9	20	71	2	2.2	1-6	10	7	41
5	Bealana	Boeny	Andranofasika	-16.373	46.652	2009	Aug to Sep	3	3	3	9	15	57	6	1.7	1-7	6	7	54
6	Vavan'ny marovoy	Boeny	Andranofasika	-16.283	46.914	2009	Aug	3	3	3	9	3	6	0	0.3	1-3			
7	Mahajanga	Boeny	Belobaka	-15.627	46.388	2009	Aug to Sep	2	1	1	2	2	11	2	1.0	4-7	1	1	50
8	Mariarano	Boeny	Mariarano	-15.482	46.686	2009	July	3	4	2	12	37	138	13	3.1	1-7	12	21	64
9	Mifoko	Sofia	Mahadirodoka	-15.123	47.098	2009	Nov	2	5	2	10	29	104	10	2.9	1-7	13	6	32
10	Marosakoa	Boeny	Mariarano	-15.434	46.633	2010	Aug	2	3	3	6	11	47	0	1.8	3-6	9	1	10
11	Namakia	Boeny	Mariarano	-15.311	46.815	2010	Aug	3	3	3	9	31	102	0	3.4	2-8	21	4	16
12	Ambatolama-Marohariva	Sofia	Analalava	-14.921	47.709	2011	Jul	2	2	2	4	10	36	2	2.5	1-6	6	3	33
27	Ambobaka	Boeny	Boanamary	-15.807	46.386	2011	May	1	3	3	3	0	0	0					
13	Ampombilava	Sofia	Ampandriankilandy	-15.007	48.110	2011	Jul	1	4	3	4	1	2	0	0.3	2-2			
14	Ampoboboka	Sofia	Ampandriankilandy	-15.039	48.213	2011	Jul	3	4	2	12	5	9	0	0.4	2-3	1	1	50
15	Anjiamangirana	Boeny	Bekobay	-15.632	46.890	2011	May	3	3	3	9	40	128	0	4.4	1-6	14	16	53
16	Ankaramikely	Sofia	Anjiamangirana I	-15.186	47.738	2011	Sep	3	3	3	9	9	26	3	1.0	2-4	7	1	13
17	Befandrama	Sofia	Analalava	-14.774	47.753	2011	Jul	2	4	3	8	19	48	5	2.4	1-8	6	8	57
18	Befandrama (SOFIA)	Boeny	Ambalakida	-15.781	46.665	2011	June	1.5	3	3	4.5	6	23	0	1.3	3-5	4	2	33
19	Bemololo	Sofia	Analalava	-14.843	47.756	2011	Jul	2	4	4	8	12	38	3	1.5	1-7	7	0	0
20	Bora	Sofia	Tsarahasina	-15.659	47.549	2011	Aug	2	3	3	6	4	7	0	0.7	1-1	1	0	0
21	Marosakoa-Ambobakely	Sofia	Ambodimandresy	-14.813	48.187	2011	Jul	1	1	1	1	1	3	0	1.0	3-3			
22	Narindra	Sofia	Antsakanalabe	-15.252	48.298	2011	Jul	1	2	1	2	1	2	0	0.5	2-2	0	1	100
23	Tsinjorano	Sofia	Marovantolena	-15.330	47.641	2011	Aug	2	4	3	8	8	28	0	1.0	2-5	2	5	71
24	Tsinjorano	Sofia	Analalava	-14.807	47.402	2011	Aug	5	4	4	20	28	87	8	1.4	1-6	12	9	43
25	Tsinjorano	Sofia	Tsinjoria	-15.456	47.418	2011	Aug	3	4	3	12	29	95	10	2.4	2-7	14	9	39
26	Tsinjorano	Boeny	Ambalakida	-15.845	46.776	2011	Jun	2	5	4	10	7	23	0	0.7	2-4	1	5	83
	Total							65	11		221	418	1409	92					

(Moat & Smith 2007, and (3) available satellite images (Google Earth®; Landsat). The principal aim of our presence in the field was to collect fecal samples for future genetic analyses from as many forest fragments as possible in the full previously known distribution range of Coquerel's sifaka. Sites were surveyed by several 2–3 member teams composed of 1–2 trained field researchers and a local guide, during 2 to 6 mo periods of the dry season each year between July 2009 and August 2011 (Table 2). Diurnal surveys of forest fragments, forest corridors, riparian forests, and mango- and tamarind-dominated tree groves surrounding villages and cultivated areas were conducted on and/or off existing trails, with observers walking slowly (~2 km h⁻¹) looking and listening for lemur presence. Teams spread out in a star-like pattern (to avoid overlapping of several teams) every morning with the objective of visiting an area previously identified on printed maps or satellites images. Guides (usually local farmers) were allocated to the different teams depending on their self-reported knowledge of the respective areas. During the survey each team could use trails or not and follow the guide's suggestions (in some areas the guides knew exactly where the sifaka groups would be) as long as the team stayed in the predefined area of survey.

For each observation of Coquerel's sifaka, group size, presence of newborns, support tree genus or species and geographic position (with Garmin® Etrex-H GPS, allowing a maximum error of 5 m and using the WGS84 referencing system) were recorded. When a group was spotted, the team usually spent 20 to 45 min collecting fresh fecal samples from individuals. Consequently, the survey was not adapted for abundance estimation (i.e. in forests with high encounter frequencies, a team could spend almost all of its time sampling feces, while in sites with low encounter frequencies we sometimes surveyed a large area without spotting any lemurs). Since our principal aim was to identify and sample existing populations, no attempt was made to use distance-sampling methods (except in Ankarafantsika, see Kun-Rodrigues et al. 2014), which are significantly more time consuming. However, we calculated relative encounter frequency per site, dividing the number of observations by the survey effort (number of survey days × number of teams involved). These easily calculated numbers give a rough idea of the relative importance of the population of each visited site. Nevertheless, they are not as accurate as (and cannot be compared with) encounter rates calculated from more standardized surveys, or of density estimated from line transect distance sampling surveys.

RESULTS

We observed Coquerel's sifakas at 26 sites (Table 2, Fig. 1) out of a total of 27, which included 15 newly visited forests. The only site with no observation of *Propithecus coquereli* was Ambatolama-Marohariva (Site 27) close to the town of Mahajanga. In addition, we report observations of *P. coquerel* at 4 additional sites (G. Rakotoarisoa and S. Wohlhauser pers. comm., Table 1), thus extending to 19 the number of new survey sites. The highest encounter frequencies (in group per day) were recorded for Mifoko, Mariarano, Analabe, Andranoboka and Anjajavy (Table 2, Fig. 1). Of the 27 (~44 %) localities 12 had relatively low encounter frequency, with values ≤1 (i.e. survey teams spotted only one or less sifaka group per day of survey on average; Table 1). The proportion of groups encountered on introduced tree species was high and comprised more than half of the observation in some sites, such as Mariarano (Table 2).

DISCUSSION

Distribution

Altogether, our results confirm the presence of *Propithecus coquereli* in its previously described distribution range, between the Betsiboka and Maevarano watersheds (Wilmé et al. 2006, 2012, Mittermeier et al. 2010; Fig. 1). Despite 78 d of survey over 3 dry seasons of field work, we did not have enough time to visit the areas between the Sofia and Bemarivo rivers, where the species has twice been reported to be absent (Ralison 2000, Gilbert Rakotoarisoa pers. comm.; Table 1). Similarly, the southern part of the inter-river system between the Bemarivo and Betsiboka rivers, where little is known about the presence of the species, still requires surveys. In this area, a recent survey (Rakotonirina et al. in press) reported the presence of Coquerel's sifaka ~90 km south of the previous southernmost observations, hence extending the distribution range of the species. This means that, despite the large size and relative conspicuousness of this diurnal lemur species, uncertainties remain regarding its distribution. Future research on Coquerel's sifaka distribution should focus on determining the western limits of the distribution range, especially in the western part of the 3 inter-river systems from Sofia to Betsiboka (Fig. 1).

It is still unclear why the distribution of *P. coquereli* should stop at its current northern limit (the Mae-

varano river, Fig. 1). Indeed, most sifakas (except *P. perrieri* and *P. tattersalli*) have distributions whose northern and southern limits are contiguous with those of generic sifaka species (Wilmé et al. 2006, Mittermeier et al. 2010). The closest northern sifaka sister species (from the western sifaka clade, Mayor et al. 2004) is *P. tattersalli*, which is located in the far northeast of Madagascar. The apparent gap between the occurrence of *P. coquereli* and *P. tattersalli* requires an explanation, be it climatic, ecologic, geographic or anthropogenic (Quéméré et al. 2012). Archaeological efforts in these ‘gap regions’ could help us understand how the current distribution of sifakas species has been shaped in the recent past.

Despite being present in almost all surveyed localities, sifakas were rare in nearly half of them (12 out of 27; ~44%), with survey teams spotting at most 1 sifaka group per day of survey (group encounter frequency ≤ 1 , Table 1). Moreover, in some sites located close to Mahajanga, we found that Coquerel’s sifakas were still present in very small degraded and anthropogenically disturbed tree groves (Site 7) largely because they were fed and protected by hotel personnel. In another site, they had probably disappeared recently (Site 27). The increasing urbanization around Mahajanga does not provide much hope for the persistence of the species in the area.

We found a group of *P. coquereli* in a thin riparian forest north of the Bora special reserve (Site 21). This was a good sign given the alarming situation in the reserve reported by Koenig & Zavaosa (2006) and that the last of the 3 studies conducted in the area reported the absence of sifakas (Randrianambinina et al. 2003, Olivieri et al. 2005, Koenig & Zavaosa 2006). Nevertheless, the Bora special reserve was not extensively surveyed during our study, and the only sifaka group observed was encountered after more than 6 km of survey. Moreover, the northeastern sites (Sites 13, 14, 16, 20, 21, 22, and Report 28) appear to harbor small numbers belonging to small forest fragments and probably isolated populations which may not be of viable size and are probably at a high risk of extinction in the coming decades.

A recent distance sampling survey conducted in Ankarafantsika National Park showed that despite density variation between sites (from ~5 to ~93 ind. km⁻²), the population size at the Park scale may still be relatively large (~47 000 ind.) and thus probably demographically viable (Kun-Rodrigues et al. 2014). Nevertheless, most of the surveyed forests reported here have a much smaller area and lower connectivity than the Ankarafantsika National Park (Moat & Smith 2007). Although only a study combining den-

sity estimates over a large set of sites and population size estimates (as conducted for *P. coronatus*; Salmona et al. in press) would enable us to assess the potential viability of each population, the encounter frequencies (Table 2) can give a rough ideas of the situation. Populations in geographically isolated sites with low and patchy forest cover and with low encounter frequencies should consequently be considered at risk.

Throughout the surveyed range, we found that Coquerel’s sifakas were using both native and degraded forests (Table 2). They were frequently observed close to or in inhabited areas (within villages, in trees interspersed between groups of houses). Moreover, locals frequently mentioned that sifakas come during the dry season to feed on mango and tamarind trees. Due to the non-systematic survey methods, it is difficult to make quantitative statements about Coquerel sifaka forest and habitat uses. Although their diet is known to be diverse (Richard 1978a) and their habitat choice to be flexible (Ganzhorn 1987), it may be useful to present here different non-mutually exclusive hypotheses that could explain the observations of Coquerel’s sifakas in anthropogenic areas: (1) the taboos traditionally protecting sifakas from hunting and consumption in the Sakalava ethnic group (Nicoll & Langrand 1989, García & Goodman 2003) are still maintained and allow sifakas to maintain high population densities close to villages; (2) high rates of deforestation (MEFT, USAID, CI 2009) reduce habitat in these areas and may force sifaka populations to use anthropogenic areas and introduced tree species; (3) food and water availability may be limited during the dry season (when our surveys took place) in both partially degraded or non-degraded forests, hence favoring seasonal movements of Coquerel’s sifaka groups towards introduced tree species and anthropogenic areas.

Conservation implications

Preliminary results from this survey were used during the IUCN SSC lemur Red List reassessment meeting in Antananarivo in 2012, to help in updating the conservation status of *Propithecus coquereli* (Schwitzer et al. 2013, 2014). We confirm that Coquerel’s sifaka is still present in most forest fragments and riparian forests of its large and highly fragmented distribution range. With such a large distribution range, the species should be used as an umbrella species for the conservation of the north-

western forest ecosystems (Wilmé et al. 2012). In fact, over its distribution range it co-occurs with 15 lemur species including the Critically Endangered *Eulemur mongoz*, and 10 Endangered species (Schwitzer et al. 2013). Moreover, the protection of the forest fragments of this large area could particularly benefit 6 species endemic to that region: 3 sportive lemurs (*Lepilemur edwardsii*, *L. otto* and *L. grewcockorum*) and 3 mouse lemurs (*Microcebus ravelobensis*, *M. bongolavensis* and *M. danfossi*), which have relatively small distribution ranges (Mittermeier et al. 2010). Considering that sportive lemurs are among the easiest lemur species to catch, that there have been recent reports of its consumption, and that they do not benefit from traditional taboos protecting them, increased conservation efforts in these 3 sub-region may help their conservation.

Recently, in the distribution range of *P. coquereli*, 2 site-based action plans were proposed (for the Ankarafantsika and the Anjiamangirana/Marosely sites; Schwitzer et al. 2013, 2014). Despite the fact that one of these plans covers probably the largest population of Coquerel's sifaka in its last main refugium (the Ankarafantsika National Park (Kun-Rodrigues et al. 2014), we do believe that only a metapopulation conservation action plan (as suggested for *P. coronatus*; King et al. 2012) including all existing protected areas and covering the known distribution of *P. coquereli* would allow its efficient long-term conservation, and would benefit all the threatened biodiversity sharing its habitat. Within the distribution range of *P. coquereli* we identified 10 existing protected and/or managed areas (Table 3) which should be supported in such an action plan. Moreover we identified potential sites for conservation projects (Table 3). Efforts could focus first on maintaining and/or restoring the last northeastern populations (Sites 13, 14, 16, 20, 21). Second, efforts could take advantage of the existing good coverage of protected areas in the region between the Betsiboka River, the Mahajamba Bay and the Ankarafantsika National Park. In that region the additional protection/management of Befandrama, Tsinjorano, Andranoboka (Sites 18, 36, 15) could enable the creation of a dense

regional network and benefit Coquerel's sifaka conservation. Moreover, further research is urgently required to (1) identify *P. coquereli*'s presence in forests that have not been visited yet, (2) obtain accurate estimates of population structure and size, and (3) ascertain the current level of connectivity between sites and its impacts on the viability of sifaka's populations in the wild. As suggested at a national scale by Schwitzer et al. (2014), specific site-based actions that can be carried out by conservationists, researchers, and local communities, can be less expensive than national initiatives (Schwitzer et al. 2013) and could also be an efficient solution for a such metapopulation-based action plan.

In northwestern Madagascar, savannas and bush fires are widespread during the long dry season and represent a major driver of deforestation and open habitat maintenance (Kull 2002, Jacquin et al. 2010). Habitat loss is also driven by the strong charcoal demand from the middle- and large-sized towns of the region (Schwitzer et al. 2013, Kun-Rodrigues et al. 2014) and by slash and burn agriculture (J. Salmona pers. obs.). While taboos traditionally protecting sifaka from poaching and consumption are strong in the Sakalava and Tsimihety ethnic groups

Table 3. Existing and suggested protected or managed areas in the range of *Propithecus coquereli*. For site and report numbers see Tables 2 and 1, respectively. MNP: Madagascar National Parks (formerly ANGAP), DGEF: Direction Régionale de l'Environnement et des Forêts, CI: Conservation International, NGO: Non Governmental Organisation, MATE: Man and the Environment. Numbers in 'Sites' column refer to numbers in Table 2 and to red numbers in Fig. 1. This table probably overlooks several community based (COBA) conservation projects managed locally

Area	Project Manager/ Associate	Sites
Existing areas		
Anjajavy	Anjajavy Hotel	2
Anjiamangirana	MadagascarAye-Aye Fund	16
Ankarafantsika National Park	MNP	3, 4, 5, 6
Bongolava forest corridor	DGEF-CI	20
Bora Special Reserve	MNP	21
Mariarano	University of Mahajanga	8
Marosakoa	NGO MATE	10
Mifoko	Aqualma	9
Namakia	NGO MATE	11
Narindra peninsula	Unima	23
Potential areas		
Befandrama	Suggested	18
Tsinjorano	Suggested	36
Andranoboka	Suggested	15
Tsiningia	Suggested	25
Marovantaza	Suggested	23
Ambobaka-Ampombilava	Suggested	13, 14
Ambarijeby-Amkaramikely	Suggested	12, 17, 19

(Nicoll & Langrand 1989, García & Goodman 2003, Ravoahangy et al. 2008), some cases of poaching have been reported in the region (García & Goodman 2003, Jenkins et al. 2011, Wilmé et al. 2012). During our survey, cases of leisure hunting (by people from neighboring or more distant towns) were reported in areas easily accessible from Mahajanga, as similarly reported for *P. coronatus* (Salmona et al. in press). Consequently, conservation efforts could focus on implementation of alternatives to (1) savanna fires in the dry season (fires are used to promote cattle grazing), (2) charcoal production and consumption, (3) slash and burn agriculture, and (4) bushmeat consumption.

Acknowledgements. We thank CAFF/CORE, the 'Direction Générale de l'Environnement et des Forêts', Madagascar National Park, the NGO 'l'Homme et l'Environnement' (in particular O. Behra, S. Blanchais) and the Aye-aye Foundation, the 'Société Verama' (in particular X. Metz), the Anjavavy Hotel (in particular C. de Foucault), the 'Société Aqualma' for giving us permission and helping us to conduct the field work. Financial support for this study was provided by the 'Fundação para a Ciência e a Tecnologia' (PTDC/BIA-BEC/100176/2008, PTDC/BIA_BIC/4476/2012 and SFRH/BD/64875/2009), the 'Institut Français de la Biodiversité' and the 'Fondation pour la Recherche sur la Biodiversité', the GDRI Madagascar, the 'Laboratoire d'Excellence' (LABEX) entitled TULIP (ANR-10-LABX-41), and the 'Instituto Gulbenkian de Ciência'. The field work was possible thanks to the continuous support of the Département de Biologie Animale et Ecologie, University of Mahajanga, the University of Antsiranana, and the Fanamby NGO (in particular S. Rajao-belina, S. Wohlhauser and V. Rasoloarison). We also thank A. Zaramody for his help and field advice. This study was conducted in agreement with the laws of the countries of Portugal, France and Madagascar. We are grateful to the editor Anna Nekaris and the reviewers for their detailed, constructive and helpful comments which greatly helped improve the quality and clarity of the manuscript.

LITERATURE CITED

- Albignac R (1981) Lemurine social and territorial organization in a north-western Malagasy forest (restricted area of Ampijoroa). In: Chiarelli AB, Corruccini RS (eds) Primate behavior and sociobiology. Springer, Berlin, p 25–29
- Ganzhorn JU (1987) A possible role of plantations for primate conservation in Madagascar. *Am J Primatol* 12: 205–215
- Ganzhorn JU (1988) Food partitioning among Malagasy primates. *Oecologia* 75:436–450
- García G, Goodman SM (2003) Hunting of protected animals in the Parc National d'Ankarafantsika, north-western Madagascar. *Oryx* 37:115–118
- IUCN (2013) 2013 IUCN Red List of Threatened Species, Version 2013.2. www.iucnredlist.org
- Jacquín A, Sheeren D, Lacombe JP (2010) Vegetation cover degradation assessment in Madagascar savanna based on trend analysis of MODIS NDVI time series. *Int J Appl Earth Obs Geoinf* 12:S3–S10
- Jenkins RKB, Keane A, Rakotoarivelo AR, Rakotomboavonjy V and others (2011) Analysis of patterns of bushmeat consumption reveals extensive exploitation of protected species in eastern Madagascar. *PLoS ONE* 6:e27570
- King T, Rakotonirina LH, Rakotoarisoa AH, Ravaloharimanitra M, Chamberlan C (2012) Projet Tsibahaka: conserving the crowned sifaka *Propithecus coronatus*. *Lemur News* 16:32–34
- Koenig P, Zavaosa A (2006) Totale disparition du Propithecus de Coquerel (*Propithecus verreauxi coquereli*) du nord de la réserve spéciale Bora (Province de Mahajanga). *Lemur News* 11:38
- Kull CA (2002) Madagascar aflame: landscape burning as peasant protest, resistance, or a resource management tool? *Polit Geogr* 21:927–953
- Kun-Rodrigues C, Salmona J, Besolo A, Rasolondraibe E, Rabarivola C, Marques TA, Chikhi L (2014) New density estimates of a threatened sifaka species (*Propithecus coquereli*) in Ankarafantsika National Park. *Am J Primatol* 76:515–528
- Mayor MI, Sommer JA, Houck ML, Zaonarivelo JR and others (2004) Specific status of *Propithecus* spp. *Int J Primatol* 25:875–900
- McGoogan KC (2011) Edge effects on the behaviour and ecology of *Propithecus coquereli* in Northwest Madagascar. PhD thesis, University of Toronto
- MEFT (Ministère de l'Environnement des Forêts et du Tourisme), USAID, CI (Conservation International) (2009) Evolution de la couverture de forêts naturelles à Madagascar 1990–2000–2005. Report by MEFT, USAID, CI. Available at http://pdf.usaid.gov/pdf_docs/pbaaa153.pdf
- Mittermeier RA, Ganzhorn JU, Konstant WR, Glander K and others (2008) Lemur diversity in Madagascar. *Int J Primatol* 29:1607–1656
- Mittermeier RA, Louis EE, Richardson M, Schwitzer C and others (2010) Lemurs of Madagascar, 3rd edn. Conservation International, Washington, DC
- Moat J, Smith P (2007) Atlas of the vegetation of Madagascar/Atlas de la végétation de Madagascar. Kew Publishing, Royal Botanic Gardens Kew, London
- Nicoll ME, Langrand O (1989) Madagascar: revue de la conservation et des aires protégées. WWF-Fonds Mondial pour la Nature, Gland
- Olivieri G, Craul M, Radespiel U (2005) Inventaire des lémuriens dans 15 fragments de forêt de la province de Mahajanga. *Lemur News* 10:11–16
- Petter JJ (1962) Recherches sur l'écologie et l'éthologie des lémuriens malgaches. *Mem Mus Natl Hist Nat Sér A* 27: 71–84
- Quéméré E, Amelot X, Pierson J, Crouau-Roy B, Chikhi L (2012) Genetic data suggest a natural prehuman origin of open habitats in northern Madagascar and question the deforestation narrative in this region. *Proc Natl Acad Sci USA* 109:13028–13033
- Radespiel U, Raveloson H (2001) Preliminary study on the lemur communities at three sites of dry deciduous forest in the Réserve Naturelle d'Ankarafantsika. *Lemur News* 6:22–24
- Rakotonirina LHF, Rajaonson A, Ratolojanahary JH, Missirli JM, Fara LR, Andriamanajanirina M, King T (2013) Southern range extensions for the critically endangered black-and-white ruffed lemur *Varecia variegata* and greater bamboo lemur *Prolemur simus*. *Primate Conserv* 26:49–55
- Rakotonirina LH F, Rakotoarisoa AH, Rakotondrabe R,

- Razafindramanana J, Ratsimbazafy J, King T (in press) A preliminary assessment of sifaka (*Propithecus* spp.) distribution, chromatic variation and conservation in central Madagascar. *Primate Conserv* 28. Available at www.primatesg.org/storage/pdf/PC_Rakotonirina_et_al_Sifaka_distribution.pdf
- Ralison JM (2000) Observations of lemurs in the Réserve Spéciale de Tampoketsa-Analamaitso. *Lemur News* 5:35
- Rambintintsoa A, Zaonarivelo JR, Randriamampionona R, Razafindraibe JFX, Brenneman RA, Louis EE Jr (2006) A preliminary study on resident lemur populations in the Mariarano Classified Forest. *Lemur News* 11:21–24
- Randrianambinina B, Rasoloharijaona S, Rakotosamimanana B, Zimmermann E (2003) Inventaires des communautés lémurienne dans la Réserve Spéciale de Bora au nord-ouest et la forêt domaniale de Mahilaka-Maromandia au nord de Madagascar. *Lemur News* 8:15–18
- Randriatahina GH, Rabarivola JC (2004) Inventaire des lémurien dans la partie nord-ouest de Madagascar et distribution d'Eulemur macaco flavifrons. *Lemur News* 9: 7–9
- Ravaloharimanitra M, Ratolojanahary T, Rafalimandimby J, Rajaonson A and others (2011) Gathering local knowledge in Madagascar results in a major increase in the known range and number of sites for critically endangered greater bamboo lemurs (*Prolemur simus*). *Int J Primatol* 32:776–792
- Ravoahangy A, Andriamaharoa HE, Randrianaina LA, Josso ATS, Raharimampionona J, Birkinshaw C (2008) Preliminary inventory of lemurs at ten priority sites for plant conservation. *Lemur News* 13:40–43
- Richard A (1974) Intra-specific variation in the social organization and ecology of *Propithecus verreauxi*. *Folia Primatol* 22:178–207
- Richard AF (1978a) Variability in the feeding behavior of a Malagasy prosimian, *Propithecus verreauxi*: Lemuriformes. In: Montgomery E, Thorington R (eds) *The ecology of arboreal folivores*. Proc Nat Zool Symp 1. Smithsonian Institution Press, Washington, DC, p 519–533
- Richard AF (1978b) Behavioral variation: case study of a Malagasy lemur. Associated University Presses, Cranbury
- Salmona J, Rasolondraibe E, Jan F, Besolo A and others (in press) Conservation status and abundance of the crowned sifaka (*Propithecus coronatus*). *Primate Conserv* 28. Available at www.primatesg.org/storage/pdf/PC_Salmona_et_al_P_coronatus.pdf
- Schmid J, Rasoloarison RM (2002) Lémuriens de la Réserve Naturelle Intégrale d'Ankarafantsika, Madagascar. *Conserv Int Washington, DC Bull Biol Assess* 23:73–82
- Schwitzer C, Mittermeier R, Davies N, Johnson S and others (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
- Schwitzer C, Mittermeier R, Johnson S, Donati G and others (2014) Averting lemur extinctions amid Madagascar's political crisis. *Science* 343:842–843
- Sussman RW (1977) Distribution of the Malagasy lemurs Part 2: *Lemur catta* and *Lemur fulvus* in southern and western Madagascar. *Ann NY Acad Sci* 293:170–184
- Weisrock DW, Rasoloarison RM, Fiorentino I, Ralison JM, Goodman SM, Kappeler PM, Yoder AD (2010) Delimiting species without nuclear monophyly in Madagascar's mouse lemurs. *PLoS ONE* 5:e9883
- Wilmé L, Goodman SM, Ganzhorn JU (2006) Biogeographic evolution of Madagascar's microendemic biota. *Science* 312:1063–1065
- Wilmé L, Ravokatra M, Dolch R, Schuurman D, Mathieu E, Schuetz H, Waeber PO (2012) Toponyms for centers of endemism in Madagascar. *Madag Conserv Dev* 7:30–40

Editorial responsibility: Anna Nekaris,
Oxford, UK

Submitted: January 20, 2014; Accepted: June 2, 2014
Proofs received from author(s): September 11, 2014