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New Density Estimates of a Threatened Sifaka Species (*Propithecus coquereli*) in Ankarafantsika National Park

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Short title: *P. coquereli* abundance in Ankarafantsika

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ABSTRACT

Propithecus coquereli is one of the last sifaka species for which no reliable and extensive density estimates are yet available. Despite its Endangered conservation status [IUCN, 2012] and recognition as a flagship species of the northwestern dry forests of Madagascar, its population in its last main *refugium*, the Ankarafantsika National Park (ANP), is still poorly known. Using line transect distance sampling surveys we estimated population density and abundance in the ANP. Furthermore we investigate the effects of roads, forest edge, river proximity and group size on sighting frequencies and density estimates. We provide here the first population density estimates throughout the ANP. We found that density varied greatly among surveyed sites (from 5 to ~100 ind/km²) which could result from significant (negative) effects of roads, and forest edge, and/or a (positive) effect of river proximity. Our results also suggest that the population size may be ~47,000 individuals in the ANP, hinting that the population likely underwent a strong decline in some parts of the park in recent decades, possibly caused by habitat loss from fires and charcoal production and by poaching. We suggest community based conservation actions for the largest remaining population of Coquerel's sifaka which will (i) maintain forest connectivity, (ii) implement alternatives to deforestation through charcoal production, logging and grass fires, (iii) reduce poaching, and (iv) enable long term monitoring of the population in collaboration with local authorities and researchers.

KEYWORDS

Propithecus coquereli; distance sampling; population density; abundance; edge effect

SHORT TITLE

***Coquerel's sifaka* abundance in Ankarafantsika**

INTRODUCTION

Madagascar has been identified as the region with the world's highest primate conservation priorities at the species, genus, and family level [Mittermeier et al., 2010]. Many lemurs such as sifakas (genus *Propithecus*) are emblematic of the island and may act as umbrella species for the conservation of other species, regions or habitats. This is the case for Coquerel's sifaka (*Propithecus coquereli*), and especially true in the Ankarafantsika National Park (ANP) which retains the largest *P. coquereli* population in the last large forest of northwestern Madagascar. Nevertheless, basic data on its ecology, distribution and population size are still missing. Given that the northwest of Madagascar is highly and increasingly fragmented and that many species are threatened by habitat loss and hunting [Mittermeier et al., 2010], an update is urgently needed to determine whether Coquerel's sifaka is still present and to estimate population density and size to identify conservation priorities and to develop management plans.

P. coquereli is one of the only *Propithecus* species for which extensive and reliable density estimates are not yet available [reviewed in Salmona et al., 2013] (Table I). The species is distributed from the Betsiboka River to the Sofia River in the northwestern region of Madagascar [Mittermeier et al., 2010]. Despite a rather large geographic distribution, Coquerel's sifaka actually survive in a mosaic of fragmented dry forests separated by wide open landscapes.

The ANP is managed by the ANGAP/MNP (Association Nationale pour la Gestion des Aires Protégées/Madagascar National Parks), and people inhabit areas around the national road that crosses through the park and areas near the park boundary. In the ANP, forest loss is mainly driven by fires, logging for charcoal production or construction, slash-and-burn agriculture, domestic livestock grazing [Radespiel & Raveloson, 2001], and root gathering [JS, AB, ER, personal observation]. Razafy Fara [2003] estimated a deforestation rate of 37.43 km^2 per year in the ANP over a period of 44 years (1955-1999), such that ~45% of the surface of the ANP was covered by savanna in 1999. Furthermore, Garcia & Goodman [2003] reported an official *Raffia* exploitation area near Antsiloky Lake. Finally, despite the prohibition of hunting in the protected area and both hunting and eating sifaka being subject to a traditional taboo for most local people, *P. coquereli* was one of the most consumed vertebrates by *Raffia* collectors [Garcia & Goodman, 2003]. Razafimanahaka et al. [2012] recently reported that over 20% of the inhabitants admitted to eating sifaka in the previous year in the commune of Tsiningia.

Although the IUCN has listed *P. coquereli* as Endangered since 1996 [IUCN, 2012], it is still thought to be common in the ANP [Mittermeier et al., 2010]. The only density estimates, dating from 1974 [Richard, 1978] and 1981 [Albignac, 1981], were extrapolated from limited behavioral data (home range size) and confined to the location of Ampijoroa. Since 1997, several authors have recorded encounter rates [Radespiel & Raveloson, 2001; Schmid & Rasoloarison, 2002; Olivieri et al., 2005] and, in 1997, Schmid & Rasoloarison [2002] attempted to estimate Coquerel's sifaka density, but did not actually publish density estimates (Table II). Overall, there is still very little information on *P. coquereli* both within and outside the ANP. There was thus an urgent need to determine more robust density and abundance estimates of *P. coquereli* based on several locations within its last main *refugium*, the ANP.

Researchers generally obtain density and population size estimates of lemurs – and more specifically of sifaka species – through line transect distance sampling surveys [e.g. Müller et al., 2000; Kelley et al., 2007; Quéméré et al., 2010; Meyler et al., 2012; Salmona et al., 2013]. Here we followed a field approach similar to the one used by Quéméré et al. [2010] and Salmona et al. [2013] to estimate the density and abundance of *P. coquereli* in the ANP. A second objective was to test possible effects of geographical features on *P. coquereli* density. A last objective was to compare four commonly-used methods as in Meyler et al. [2012]: (a) the mean perpendicular distance method (MPD) [Gates et al., 1968]; (b) the Kelker method [Kelker, 1945] (c) the Müller method [Müller et al., 2000]; and (d) a conventional distance sampling analysis (CDS) [Buckland et al., 2001]. To our knowledge, these are the first density and population size estimates for *P. coquereli* incorporating distance sampling data from several sites of the ANP, and the first attempt to compare different estimation approaches for a large, group living, diurnal lemur species.

METHODS

Study Area

We surveyed transects in the Ankarafantsika National Park (ANP), northwest Madagascar (16.300 S, 46.817 E; Fig. 1). The Mahajamba and Betsiboka Rivers delimit the park in the north-east and south-west respectively. The ANP has an area of 1,350 km^2 [Conservation International, 1994] and consists of a mosaic of dry deciduous forests, savannas and small valleys. Sifakas are limited to forested habitat, which represented ~1000 km^2 in 2000-2001 (our estimates from data of Moat & Smith [2007]).

From August to early September 2009 we visited four localities (Fig. 1): Beronono, located at the extreme north-east of the ANP; Vavan'i Marovoay in the center-east;

Ampijoroa, located along the "Route Nationale 4" (RN4) that crosses the ANP; and Bealana situated in the extreme south-west of the Park.

Field Procedures

At each site, we delineated three to six transects regularly marked with flagging tape. In Bealana and Ampijoroa, we oriented transect lines from the edge to the interior of forest fragments using aerial maps. Because of field constraints, the remaining transect lines did not always start at the edge of a forest but nevertheless sampled locations at various distances from the edges, and avoided savannas and burnt forest patches. Transect length varied from 675 m to 2,747 m (Table III). We surveyed transects 4–6 times during 2–3 days, from 7:30 a.m. to 11 a.m. and 12:30 p.m. to 4 p.m., with an average velocity of 0.58 $km.h^{-1}$ (SD=0.24). Every day, several transects were followed by different two-member teams. On the following day, one member of each team changed team and transect to avoid observational biases among transects and to ensure that at least one team member had already walked a specific transect [Quéméré et al., 2010]. When we observed a sifaka group, we collected the following data: date, time, group size, GPS position, sighting distance of the center of the group (AOD, animal-to-observer distance) with a measuring tape, and angle to compute perpendicular distances (PD) to the transect. For each site, we calculated the total effort length, i.e., the length of each transect times the number of surveys, summed across transects.

Density and Population Size

Line transect distance sampling density estimates are obtained by dividing the number of animals seen *n* by *esa,* the effective sampling area, i.e. $\widehat{D}$=n/*esa*, where *esa* is the product of the length of transect *L* and twice the estimate of the effective strip (half) width (*ESW*). We used both model-based and non-model-based methods to obtain *ESW* and hence estimate sifaka densities, to (i) provide values comparable with studies using Müller, MDP or Kelker methods and to (ii) compare methods.

Non-model-based methods are still widely used to estimate primates and lemur density [e.g. Müller et al., 2000; Lehman et al., 2006a; Rasolofoson et al., 2007; Beaucent & Fayolle, 2008; Gardner et al., 2009; Randrianambinina et al., 2010] in spite of the emergence of newer computing techniques. These methods differ only in how they estimate the effective strip width [Buckland et al., 2001; Marshall et al., 2008; Meyler et al., 2012].

The mean perpendicular distance method (MPD) [Gates et al., 1968] estimates strip width as the mean perpendicular distance (animal to transect) at which observers sighted sifakas. This method implicitly assumes that the underlying detection function is negative exponential, which presents an implausible shape under most scenarios, where a much smoother function is expected.

The Kelker [Kelker, 1945] and Müller [Müller et al., 2000] methods are histogram inspection techniques that use the shape of the distribution of observation distances (perpendicular and animal to observer distance respectively) to define a "fall-off distance" (FD) and estimate strip width. For each of these two methods, we chose the FD with a 50% drop criterion on histograms plot with bins of 4 to 10 meters. The FD was then chosen based on the frequency of the FD among, and visual inspection of the 7 histogram plots. We implemented the conventional distance sampling (CDS) method of Buckland et al. [2001] using Distance 6.0 software [Thomas et al., 2010]. This method uses a set of flexible semi-parametric functions to model a detection function, which represents the probability of detecting an animal as a function of the distance from animal to transect. We tested the uniform, hazard-rate, half-normal and negative-exponential detection functions and compared them using Akaike's Information Criterion corrected for small samples (AICc) [Buckland et al., 2001]. To avoid difficulties in fitting the tail of the detection function, we truncated 5% of the data, as recommended by Buckland et al. [2001]. We tested the effect of cluster (social group) size and period of the day (morning *vs.* afternoon) on the estimation of the detection function using the Multiple-Covariate Distance Sampling (MCDS) analysis [Marques et al., 2007]. We obtained the variance for the MCDS analysis via bootstraps with transect as the resampling unit.

Distance 6.0 does not allow for stratification when cluster size is a covariate, but we were interested in density estimates for each of the four study sites. For inference we used CDS with size bias regression: the mean group size, E(*s*), is estimated from a regression model in which *log*(cluster size) is regressed on *log*(estimated probability of detection) [Thomas et al., 2010] correcting for the fact that larger groups might be easier to detect. Density is then estimated as $\widehat{D}=E(s)n/esa$.

For all methods, despite the fact that the habitats were not fully identical between transects and between sites, no assumption was made about the relationship between density and habitat type and we calculated ANP global density estimates using the average density of the four sites, considering these as random locations representative of the whole park.

We also used the data from Schmid & Rasoloarison's [2002] *P. coquereli* distance sampling survey conducted in 1997 in three additional sites (Ankarokaroka, Antsiloky and Tsimaloto). The information available in their study allowed us to use only the

MPD method. Due to the limited number of observations at the three sites it was not possible to estimate an ESW in each of them and we therefore estimated a single ESW that was applied to all three sites.

To test for significant differences in density between survey sites and methods, we used a modified independent samples t-test, the Z-test:

$$Z = \frac{D_1 - D_2}{\sqrt{SE(D_1)^2 + SE(D_2)^2}}$$

where D_i is the density estimate for site i; and $SE(D_i)$ represents the standard error of the D_i [Buckland et al., 2001; Bicknell & Peres, 2010], and Bonferonni correction to account for multiple comparisons. We acknowledge that the small number of transects within sites and the low number of observations for some sites leads to non-robust variance estimates, limiting the power of the test.

Finally, we estimated population size, multiplying the global density estimates by the ANP total suitable forest area for *P. coquereli*. We calculated forest area in ArcGIS v9.3, using forest layers from the Madagascar Vegetation Mapping Project [http://www.kew.org/gis/projects/mad_veg/datasets.html; Moat & Smith, 2007].

Forest Edge, River and Road Effects

To determine whether forest edges, water basins (rivers and lakes) and roads had an effect on the distribution of *P. coquereli*, we compared the number of sifaka groups encountered at different distances from these features. We calculated distances between sifaka sightings and each geographic feature using ArcGIS v9.3 and the forest data from the Madagascar Vegetation Mapping Project [Moat & Smith, 2007]. We compared group sightings (observed distribution) with the distribution of weighted survey effort (i.e. the expected distribution if the tested feature had no effect on animal distribution) using Pearson's χ^2 Test for count data with 10,000 permutations. We assigned data to two distance classes to determine the distance up to which we could detect an effect on sifaka distribution: we sequentially increased the first distance class (0-100 m, 0-200 m, 0-300 m, and so on) until there was no significant difference in frequency between the sightings and the survey effort for the first class. The second class consisted of the sightings for the remaining distances from the feature. In the absence of edge, river or road effects, we expected no difference between group sighting distribution (observed) and sampling effort distributions (expected).

We estimated the effect of the national road crossing the ANP by plotting the distance from this road for every site against site-specific densities calculated with the MPD method, a procedure that allowed us to use Schmid & Rasoloarison's [2002] data. We used linear regression to evaluate whether sifaka density responded to distance from the national road across the seven sites. As a consequence of our small number of data points for the regression, which gives low statistical power, we took marginally statistically significant slopes in consideration.

This study was made in agreement with the laws of the countries of Portugal and Madagascar. We received permission to conduct this research in Madagascar from CAFF/CORE, the "Direction Générale de l'Environnement et des Forêts" and Madagascar National Parks. This research adhered to the American Society of Primatologists principles for the ethical treatment of primates.

RESULTS

Density Estimates from Line Transect Surveys

We detected a total of 291 individuals in 73 social groups over 118 km of surveyed transects. Group size varied from 1 to 9 individuals (Table III) with an average of 4.03 ind/group (SD = 1.93). Despite considerable survey effort, only at Beronono we achieved the minimum of 40 sightings required to accurately model detection functions [Buckland et al., 2001] (Table III). The limited number of observations did not allow us to compute an ESW for each site individually. Therefore, we estimated a global ESW with pooled data, assuming similar detectability at all sites. This assumption is reasonable given that similar habitats occur at each site and that the same observers surveyed all sites during the same period. We also estimated density separately for Beronono. The very small ESW difference between Beronono and the pooled data (Table IV) estimated with the CDS analysis supports our assumption of similar detectability across sites. Using the CDS method, the low AICc differences between models did not allow us to identify clearly a best fitting detection function. We thus kept the Hazard-rate function for further analysis, previously reported to be the best detection function for *Propithecus* species in dry forest on much larger data sets [Quéméré et al., 2010; Salmona et al., 2013]. The densities from all site and methods showed considerable discrepancies, with average values per sites varying between 0.5 and 200 ind/km^2 (Table IV). Regardless of method, however, Ampijoroa and Vavan'i Marovoay sites showed markedly lower densities than Bealana and Beronono (Table IV). Differences between high density sites (Beronono and Bealana) and low density sites (Ampijoroa and Vavan'i Marovoay) were significant before applying Bonferroni correction but only differences between high density sites and Ampijoroa remained significant after Bonferroni correction (alpha= 0.0083, Table V).

Considering the CDS method as benchmark, the MPD method always produced higher density estimates (twice higher), whereas the Kelker estimates did not depart much from it. The Müller method failed to give similar estimates for Ampijoroa (Table IV), one site out of four, the site with the lowest amount of sightings. For some of the sites tested the estimated densities using the MPD method were outside the 95% confidence intervals of the CDS method, but none of the differences between methods were significant with the Z-test even without applying the Bonferonni correction. Compared to the CDS method, discrepancies in the FD for the Müller and Kelker methods led to higher discrepancies in ESW and density estimates for Beronono using either the pooled or Beronono data (Table IV).

Inclusion of cluster size as a covariate led to a clear reduction in AICc (Table VI), suggesting that cluster size positively influences detectability, *i.e.* at larger distances one is more likely to detect larger *vs*. smaller groups. By contrast, we found no significant effect of the time of the day (morning *vs.* afternoon) on the detection probability (Table VI). The MPD analysis of Schmid & Rasoloarison's data [2002] shows low density estimates ranging from 19 to 56 ind/km^2 in Ankarokaroka and Antsiloky, respectively (Table II), with a global ESW of 8.73 m.

Forest Edge, River and Road Effects

We detected a negative effect of the forest edge on sighting frequency up to 400 m from the edge of the forest (Fig. 2a). We found the same negative effect for three individual sites (Beronono, Vavan'i Marovoay and Ampijoroa), with an edge effect extending to 900 m inside of the forest for the latter two. Our sampling effort for Bealana started far from the edge (268 m) which may explain why no edge effect was apparent here. We found a positive effect of the river on sighting frequency up to 200 m when we pooled the data from all the sites (Fig. 2b). *P. coquereli* sightings frequency and density seems negatively affected by the national road proximity (Fig. 2c and 2d). Linear regression showed that population densities increased with the distance of the site from the national road (F=9.027; df=5, P=0.030; R^2=0.64; Fig. 2c).

DISCUSSION

Densities in ANP

Comparing our results with those published in studies conducted in the last decades suggests that the sifaka population in Ampijoroa underwent a major decline. Indeed, Ampijoroa, which is located on the edge of the national road, is the most surveyed ANP site (Table II). In 1962 and 1974, researchers sighted 27 and 12 groups, respectively [Petter, 1962; Richard, 1974]. In 1981 and 1988 reasonably high densities were still reported [60-75 ind/km^2; Albignac, 1981; Ganzhorn, 1988], whereas in 2001, Radespiel & Raveloson [2001] reported no sightings of sifaka (Table II). During our 2009 study and despite a larger survey effort in Ampijoroa than in other sites, we sighted only 4 groups of *P. coquereli*, and estimated a low density of only 5 ind/km^2. This is an order of magnitude less than the values found in the 1980s and less than most values found for *Propithecus* species [e.g. Norscia & Palagi, 2008; Pichon et al., 2010, Salmona et al., 2013] (Table I). It suggests that the density decreased from around 60-75 ind/km^2 in the 80s [Albignac, 1981; Ganzhorn, 1988] to 5 ind/km^2 now in Ampijoroa, a decrease of more than 90%.

In many regions of Madagascar, including the ANP, sifaka species are protected from hunting and eating by local beliefs ("*fady*"), but this "*fady*" seems to be less and less respected [Nicoll & Langrand, 1989]. Logging also appears to have increased in the last decades in the park [Radespiel & Raveloson, 2001; Garcia & Goodman, 2003]. It is very likely that human activities have reduced densities of *P. coquereli*. Nevertheless, it would be important to identify other forces that may have an influence on densities (vegetation type, micro-climate) beyond those derived from forest exploitation (charcoal consumption, savanna fires). For instance, it is particularly surprising to find that the lowest densities are found in Ampijoroa, where the tourism administration and main research site are located. Here one would expect to find a more effective protection reflected in highest densities than in more remote places. Moreover, Ankarokaroka and Vavan'i Marovoay, the sites closest to Ampijoroa, also showed low densities and encounter rates [Radespiel & Raveloson, 2001; Schmid & Rasoloarison, 2002] (Table II). We met poachers in Vavan'i Marovoay during our surveys, and the forest was highly disturbed by humans exploiting wood, roots and *Raffia* and by fires. The low sifaka densities could therefore be caused by the presence in the ANP of poachers for whom hunting lemurs is not "*fady*" and who may use the road as an easy entry to forest resources. Moreover Vavan'i Marovoay is close to the national road, and from 2009-2013, we have noticed a tremendous number of charcoal bags for sale along the road between Andranofasika and Ambondromamy.

We realize that our conclusions are limited by the few groups sighted at Vavan'i Marovoay and Ampijoroa. Therefore, an increased survey effort, with more sites, transects per site, and repetitions per transect would be welcome in the future to improve and validate our findings.

Comparison with Studies on Other Sifaka Species

Density estimates for *Propithecus* species vary widely among species, studies, sites and over time, with values ranging from ~3 ind/km² for *P. perrieri* [Banks et al., 2007], to ~300 ind/km² for some *P. coronatus* locations [Salmona et al., 2013] (Table I). The range of densities estimated for *P. coquereli* is within the range reported for the other sifakas, with the lowest densities comparable to the most endangered species (*P. perrieri*) and the largest values comparable to several other species.

The number of individuals of Coquerel's sifaka living in the ANP is difficult to estimate because densities appeared to vary widely across the Park. Thus, the population size estimates extrapolated from our density estimates should be considered preliminary. We present them here because absolute numbers are essential for conservation purposes. Using the average estimated by the CDS approach, population size of *P. coquereli* may be ~47,000 individuals in the ANP (Table IV). However, we note that population size extrapolation was performed using a geographical dataset produced with 1999-2001 satellite images [Moat & Smith, 2007]. If we consider the high rate of deforestation in the ANP over the last century [Razafy Fara, 2003; Dollar, 2006], the suitable habitat surface one decade later might also have decreased, and our number might represent an overestimate of the abundance of *P. coquereli*.

If we compare these values to those of other sifakas, the situation of *P. coquereli* seems better than that of the Critically Endangered *P. perrieri* population in the Analamerana special reserve for which the whole population is estimated at 915 individuals [Banks et al., 2007]. Quéméré et al. [2010] estimated ~15,000 individuals for the Critically Endangered and sister species *P. tattersalli*. For *P. coronatus*, we estimated that ~100,000 individuals may still survive across its whole distribution range [Salmona et al., 2013], with 10,000-36,000 individuals in the surveyed area (Table I).

If *P. coquereli* maintains a relatively large population in ANP, it is most likely because of the considerable size of the park. Indeed, it seems likely that the population today is considerably smaller than it was in the past. Densities in Ampijoroa decreased by about 90% since the 1970's. Also, the high discrepancies between sites with the lowest densities close to the national road suggest that the density found now in Ampijoroa is representative of a population affected by humans. If we use the Ampijoroa former densities [Albignac, 1981; Ganzhorn, 1988] as representative of the species before extensive human interference, and apply it to the whole ANP (thereby simulating values before a likely but still hypothetical population decline), we would calculate a population size of ~60-75,000 individuals in the park. It is important to emphasize that this is the largest forested area in northwest Madagascar. All other *P. coquereli* populations survive in smaller forest fragments, and are therefore more likely subject to decline and possibly extinction. In fact, if nothing is done to protect Coquerel's sifaka, densities of ~5-10 ind/km², as seen in Ampijoroa and Vavan'i Marovoay, may extend to the whole ANP. This could mean that a population that had ~60-75,000 individuals originally would decrease by ~90-95% to perhaps 5,000 individuals in the next decade or two.

Group Size, Time, Forest Edge, River and Road Effects

The MCDS analysis showed that group size in *P. coquereli* should probably be incorporated as a covariate when modeling the detection function used for density estimates. Cluster size (group size) has often been found to be a covariate when modeling detectability for other species [e.g. Zerbini et al., 2006; Arnhem et al., 2008; Braulik et al., 2012]. By contrast, the period of the day (morning *versus* afternoon) at which transect were walked did not affect density estimates (Table S2). Sifakas, like many primates, are known to have variable activity patterns during the day. They are usually more active in the morning and in the late afternoon [Richard, 1974; Mittermeier et al., 2010]. Here, the variable activity pattern does not seem to affect detectability, suggesting that increased activity at the beginning and at the end of the day may balance each other. In fact we performed our surveys over several hours of high and low activity both in the morning and in the afternoon, hence perhaps averaging out any possible effect caused by these diurnal activity shifts.

The presence of a size bias, larger groups being easier to detect, is readily accounted for by CDS, size bias regression, or MCDS, which allows the effect to be modeled. However, the effect of group size on detectability should lead to biased results from the other 3 methods we considered, because the observed group size is biased up, and the non-model-based methods fail to account for this fact. Group size could influence density estimates in other sifaka species, and in other forest dwelling species with variable group size. The best analysis would therefore be a MCDS model with cluster size as a covariate, but because Distance does not allow this, we only used here the CDS analysis with group size bias regression.

Depending on the species, forest edges can have a positive, negative or neutral effect on the distribution of individuals [e.g. Lehman et al., 2006a, 2006b, 2006c; Quéméré et al., 2010; Meyler et al., 2012]. In the case of *P. coquereli*, McGoogan [2011] found that groups tend to concentrate inside the forest, avoiding the edges in ANP. Our results confirm this tendency. There seems to be a 400 m buffer zone, which may extend up to

900 m in some locations, where the groups are less frequent. This figure is congruent with McGoogan's [2011] finding that several biotic variables, such as plant density and species richness, were greater in the interior of the forest beyond the first 400 m from the edge at Ampijoroa during dry season. These changes in food availability together with greater human presence, and hunting pressure at the edges could explain the avoidance of edges by sifakas in ANP. Additional surveys at different seasons and at more localities may help to clarify this pattern.

We were not able to disentangle site from river effects given that the distribution of *P. coquereli* regarding rivers is site specific. Nevertheless rivers appear to have a positive effect detected globally until 200 m. Rivers may be attractive to sifakas because of enhanced food availability close to the water sources during the dry season. However further studies, especially during the dry season, will be necessary to confirm this hypothesis.

We found that the national road (RN4), which crosses the ANP, had a substantial negative effect on the presence and density of *P. coquereli*. The road, which links Mahajanga to the main cities of Madagascar, including the capital, is crossed everyday by hundreds of vehicles, and facilitates human access to the forest for logging, charcoal production and hunting [JS, AB, ER, personal observation]. Assuming that hunting and logging are more likely to occur along the road and that hunted species might experience a negative edge effect [Lehman et al., 2006a], the confounded effect of road and edge could explain the low densities at Ampijoroa, and the high densities found in remote areas (i.e. Beronono and Bealana; Fig. 2c). Interestingly, Quéméré et al. [2010]

found no significant edge effect for *P. tattersalli* in the north of Madagascar, maybe because *P. tattersalli* is less hunted than *P. coquereli*, the forests are much smaller in the Loky-Manambato region and the forest experiences less charcoal production, root gathering and fires than in the ANP [JS, AB, ER, personal observation]. Indeed, Quéméré et al. [2010] suggested that when forests are small, it may become difficult to identify a "core" area.

Comparison of Methods

Altogether we found a good agreement of the Kelker, Müller to the CDS method across most sites. The mean perpendicular distance method however always showed higher density values than the CDS method, doubling even the global density for the ANP. Several authors have already cautioned against its use, especially for endangered species, because of this bias [e.g. Sterling & Ramaroson, 1996; Link et al., 2010; Meyler et al. 2012].

While the Kelker and Müller methods gave results similar to the CDS method in most cases, we nevertheless recommend the CDS method because its density estimates were relatively robust whether we used the global data set or only the Beronono data. On the contrary, the Kelker method showed a substantial increase in the density estimates when only the Beronono data were used (>30%; Table IV). We note that the crucial step of defining the FD was difficult for *P. coquereli*. The arbitrariness of the choice of the FD, which strongly influences the final density estimates, suggests that methods requiring this step should be avoided or used with caution. The Müller method, based on animal-to-observer distance, fails conceptually to represent an ESW and Buckland et al. [2010] have argued against its use. Nevertheless, since most studies on sifaka densities have used older methods (Table I), using them in parallel to the CDS method can still be useful for comparison purposes. We emphasize that the bias for the MPD is a function of the true unknown detection function (which might be different across years and/or sites), and hence, even for comparison purposes MPD might lead to erroneous conclusions.

Conservation Implications

Overall, population density seems to be decreasing in some areas of the ANP if not throughout the park. Since the recovery from demographic declines in small isolated populations is long and never certain, we can estimate that low population densities may be a major issue for *P. coquereli*, a problem exacerbated by the species' slow development and long generation time (probably between 6 and 15 years, based on data from *P. verreauxi*; [Richard et al., 2002; Lawler, 2007]). Most sifakas are easy to approach and thus easy to hunt. Despite being "*fady*" for most of the locals, Coquerel's sifaka, like other closely related species, are hunted [Garcia & Goodman, 2003; Golden, 2009; Jenkins et al., 2011; King et al., 2012; Razafimanahaka et al., 2012; Salmona et al., 2013]. Habitat loss and fragmentation may increase forest edge [Fahrig, 2002] and landscape disconnectivity. Habitat fragmentation negatively affects other sifaka species [Irwin et al., 2010] and other lemurs [e.g. Lehman et al., 2006a; Irwin et al., 2010]. From 1955 to 1999, ~80% of the ANP forest cover suffered degradation [Razafy Fara, 2003], and from 1990 to 2000 the park lost ~20% of its original forest cover [Dollar, 2006], most probably to fire, charcoal production, and root gathering. A concomitant increase in edge area would have depressed the number of sifakas.

To maintain a healthy, non-isolated and non-fragmented population in the last remaining important *refugium* of *P. coquereli*, it will be important to decrease deforestation rates. Efforts could focus on implementation of alternatives to (i) savanna fires in the dry season (fires are set to promote for cattle grazing), (ii) charcoal production and consumption, (iii) bushmeat consumption, and (iv) root gathering. Reforestation is needed to maintain connections between forest patches within the park, and between the park and forest fragments further north. Community awareness and ecological education, especially along the national road, around the park and in towns where charcoal and other forest products are purchased and consumed, would benefit the long-term conservation of the habitat. Moreover, long term monitoring of the population could allow assessing population trends and refining conservation strategy of *P. coquereli* in a near future.

Finally, we want to stress that funding is urgently needed for protected area managers to implement conservation strategies. Since the political turmoil of 2009, deforestation and hunting rates have increased tremendously in Madagascar [Patel, 2010], while international funding has been to a large extent blocked [Schwitzer, 2011; Froger & Méral, 2012]. No efficient conservation plan can be implemented in these conditions and the situation could lead to a major decrease not only of the Coquerel's sifaka populations, but also of many other endemic species inhabiting ANP and other forests of Madagascar, together with the loss of the most endangered ones [Schwitzer et al., 2013].

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Table I. Sifaka density estimates from the published literature.

Species	Site	Density (individuals /km²)	Field Method	Analysis Method	Estimated population size	Reference
P.coquereli	Ampijoroa	75	-	-	-	Albignac [1981]
	Ampijoroa	60	Home range and mean group sizes	-	-	Ganzhorn [1988]
	Ankarafantsika	5 - 93	LT-DS	CDS and other	52,123	**This study**
P.coronatus	North West	49 - 309	LT-DS	CDS	130,000 to 220,000	Salmona et al., [2013]
	Antrema	>300	Complete census	-	-	Pichon et al. [2010]
	Anjamena	172.6	LT-DS	Müller	-	Müller et al. [2000]
	Anjamena	543	Home range size	-	-	Müller [1997]
P.verreauxi	Berenty	41 - 1036	Complete census	-	-	Norscia & Palagi [2008]
	Berenty	211	-	-	-	O'Connor [1987]
P.tattersalli	Daraina region	34 - 90	LT-DS	CDS	11,000 to 26,000	Quéméré et al. [2010]
	Daraina region	17 - 28	LT-DS and Fixe Observation Point	-	6,100 to 10,000	Vargas et al. [2002]
P.edwardsi	Antserananomby	49	LT-DS	CDS	-	Kelley et al. [2007]
	Vohibola	2 - 73	LT-DS	Kelker	-	Lehman et al. [2006b]
	South Est	7.65	LT-DS	Kelker with AOD	39,528	Irwin et al. [2005]
P.diadema	Tsinjoarivo	7.61 - 20.4	Home range size	-	-	Irwin et al. [2008]
P.candidus	Makira	1.5 - 23.1	LT-DS	MPD	-	Rasolofoson et al. [2007]
	Marojejy	40 - 90	LT-DS and random walking	Min Convex Polygon	-	Sterling & McFadden [2000]
P.perrieri	Analamerana	3.11	LT-DS	Kelker	915	Banks et al. [2007]
	North	18 - 21.4	LT-DS and home range size	-	100 to 2,000	Meyers & Ratsirarson [1989]
	Analamerana	3 - 4	-	-	< 1,000	Petter et al. [1977]

Note: LT-DS: Line Transect Distance Sampling; CDS: Conventional Distance Sampling; AOD: Animal to Observer Distances; MPD: Mean Perpendicular Distance.

Table II. Summary of census studies of *Propithecus coquereli* in northwestern Madagascar.

Site	Location NS	Location EW	Protected	Year	Survey Period (month)	# groups sighted	Mean group size	Group size range	Group encounter rate (group/km)	Density (ind/km²)	Method	Reference
Ampijoroa	-16.03	46.82	Y	1962	-	27	4	-	-	-	-	Petter [1962]
				1974	-	12	5.5	4 - 10	-	-	-	Richard [1974]
				1978	-	-	5	1 - 5	-	60	Home range	Richard [1978]
				1981	-	-	-	3 - 5	-	75	-	Albignac [1981]
				2000	Sept	-	-	-	0	-	-	Radespiel & Raveloson [2001]
				2007-2008	-	4	5.6 - 7.8	5 - 8	-	-	-	McGoogan [2011]
				2009	Jul-Aug	4	2.25	1 - 4	7.86E-05	5	CDS	**This study**
Ankarokaroka	-16.34	46.79	Y	1997	Feb	2	4	3 - 5	0.33	19	MPD	**This Study** (Data from Schmid & Rasoloarison [2002])
				2000	Sept	-	-	-	0	-	-	Radespiel & Raveloson [2001]
Antsiloky	-16.23	46.96	Y	1997	Feb	4	5.3	5 - 6	0.85	56	MPD	**This Study** (Data from Schmid & Rasoloarison [2002])
Bealana	-16.37	46.65	Y	2009	Aug-Sept	23	4.77	1 - 9	1.17E-03	77	CDS	**This study**
Beronono	-16.04	47.14	Y	2009	Aug	42	3.78	1 - 8	1.41E-03	93	CDS	**This study**
Bevazaha	-16.23	47.15	Y	2000	Sept	-	-	-	0	-	-	Radespiel & Raveloson [2001]
Ste Marie	-16.12	46.95	Y	2000	Sept	-	-	-	0	-	-	Radespiel & Raveloson [2001]
Tsimaloto	-16.23	47.14	Y	1997	Feb	4	3.3	2 - 5	0.23	23	MPD	**This Study** (Data from Schmid & Rasoloarison [2002])
Vavan'i Marovoay	-16.28	46.91	Y	2009	Aug	4	4.33	2 - 6	1.49E-04	10	CDS	**This study**
Ambarijeby	-14.94	47.71	N	2004	May-Jun	-	2.2	-	0.83	-	-	Olivieri et al. [2005]
Ambodimahabibo	-15.50	47.48	N	2004	Jul-Aug	-	2	-	0.5	-	-	Olivieri et al. [2005]
Ambongabe	-15.33	47.68	N	2003	Jul-Aug	-	2.5	-	0.44	-	-	Olivieri et al. [2005]
Anjiamangirana I	-15.16	47.74	Y	2004	Sept-Oct	-	1.67	-	0.33	-	-	Olivieri et al. [2005]
Ankarafa	-14.38	47.76	Y	2004	Oct	-	-	-	0	-	-	Olivieri et al. [2005]
Bora	-14.86	48.21	Y	2004	Jun	1	2	-	0.18	-	-	Olivieri et al. [2005]
				2005	Dec	-	-	-	0	-	-	Koenig & Zavasoa [2006]
Le Croisement	-16.86	47.03	N	2003	May	-	-	-	0	-	-	Olivieri et al. [2005]
Mahatsinjo	-14.79	47.78	N	2004	Sept	-	4.5	-	0.33	-	-	Olivieri et al. [2005]
Mangatelo	-16.41	46.97	N	2003	May-Jun	-	-	-	0	-	-	Olivieri et al. [2005]
Marosakoa	-15.26	48.30	N	2004	Jul	-	-	-	0	-	-	Olivieri et al. [2005]
Mariarano	-15.48	46.69	N	2003	Jul	-	3	-	0.5	-	-	Olivieri et al. [2005]
			Y Since 2006	2006	Nov	-	-	2 - 7	-	-	-	Rambinintsoa et al. [2006]
Maroakata	-16.08	47.30	N	2003	Aug-Sept	-	-	-	0	-	-	Olivieri et al. [2005]
Tananvaovao	-15.47	46.67	N	2003	Jul-Aug	-	3.5	-	1.43	-	-	Olivieri et al. [2005]
Tsiaramaso	-15.80	47.12	N	2003	Oct	-	2.67	-	1.11	-	-	Olivieri et al. [2005]
Tsinjomitondraka	-15.66	47.12	N	2004	Aug	-	2.69	-	2.17	-	-	Olivieri et al. [2005]

695 Note: Sites above and below the horizontal line are located respectively inside outside the ANP, for both parts, sites are arranged alphabetically and data for each site is arrange chronologically. NS and EW: North-South and East-West GPS coordinates, in decimal degrees, WGS84 format. Column four (Protected), "Y" means "yes" (protected) and "N" means "no" (not protected). Group size range represents the minimum and maximum size of the group sighted during the survey. In all columns and rows, "-" means that information was not available.

700 **Table III. Description summary of *P. coquereli* survey and sightings by site.**

Site	# transects	Mean transect length (km) (SD)	Total effort length (km)	# groups sighted	Mean group size (SD)	Group size range	# individuals sighted
Total	16	1.36 (±0.54)	97.03	73	4.0 (±1.9)	1 - 9	291
Beronono	3	1.54 (±0.50)	7.33	42	3.7 (±1.7)	1 - 8	154
Vavan'i Marovoay	4	1.04 (±0.38)	20.07	4	3.8 (±2.1)	2 - 6	15
Ampijoroa	6	1.62 (±0.64)	50.87	4	2.3 (±1.5)	1 - 4	9
Bealana	3	1.04 (±0.18)	18.77	23	4.9 (±2.3)	1 - 9	113

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Table IV. Comparison of Coquerel's sifaka density estimated with different methods.

Sites	Method	Bins	FD	ESW	Density (D)						Population size (A)		
					D	95% CI Lower	95% CI Upper	SE	CV	Z-test P-value	A	95% CI Lower	95% CI Upper
All sites	Kelker	6;10	30	33.7	43.6	1.0	86.0	21.7	0.02		43,980	1,075	86,885
	Müller	8	24	24.0	41.9	0.0	84.0	21.3	0.02		42,321	121	84,522
	MPD			17.0	86.6	2.0	171.0	43.1	0.01		87,358	2,136	172,580
	CDS			25.7	46.4	2.0	90.0	22.7	0.02		46,853	1,938	91,768
Vavan'i Marovoay	Kelker				9.6	0.0	34.0	10.9	0.36				
	Müller				11.4	0.0	47.0	15.9	0.02				
	MPD				19.1	0.0	69.0	21.6	0.71				
	CDS				9.9	1.0	83.0	7.7	0.78				
Ampijoroa	Kelker				2.6	0.0	6.0	1.9	0.12				
	Müller				0.4	0.0	1.0	0.3	0.55				
	MPD				5.2	0.0	11.0	3.8	0.23				
	CDS				5.2	1.0	41.0	5	0.96				
Bealana	Kelker				83.0	7.0	145.0	35.2	0.49				
	Müller				67.7	3.0	121.0	30.2	0.02				
	MPD				164.9	15.0	288.0	69.8	0.97				
	CDS				77.4	28.0	215.0	25.4	0.33				
Beronono	Kelker			33.7	79.1	21.0	130.0	27.9	0.31	0.484			
	Kelker (Ber.)	4;5;10	20	23.5	113.3	30.0	187.0	40	0.44				
	Müller			24.0	88.2	0.0	166.0	42.7	0.02	0.879			
	Müller (Ber.)	4;5;10	20	20.0	97.9	0.0	185.0	47.6	0.74				
	MPD			17.0	157.1	41.0	259.0	55.5	0.62	0.636			
	MPD (Ber.)			13.4	199.5	53.0	329.0	70.5	0.78				
	CDS			25.7	93.3	31.0	283.0	32.4	0.35	0.945			
	CDS (Ber.)			23.7	96.5	34.0	274.0	35.4	0.37				

Note: Bins: histogram bins used for the choice of the FD value; FD: Fall of Distance; ESW: Effective Strip Width; CV: Coefficient of Variation; MPD: Mean Perpendicular Distance; CDS: Conventional Distance Sampling; Ber.: estimations specifically for Beronono data (see text), when not specified. Z-test P-values for differences between the density estimated with the global ESW and the density estimated with Beronono data only.

Table V. Comparison of CDS density estimates using the Z-test.

Site	Ampijoroa	Bealana	Beronono
Vavan'i Marovoay	0.612	0.011	0.012
Ampijoroa		**0.005**	**0.007**
Bealana			0.7

Note: P-values obtained for the Z-test comparisons of results shown in Table IV. Bold font indicates values that are significant for the Bonferroni corrected alpha value of 0.0083.

Table VI. Model selection using the DISTANCE software for density estimation.

Model	# params	AICc	ESW	D	95% CI Lower	95% CI Upper	CV
CDS Half-Normal	1	485.7	25.7	38.6	17.6	84.7	0.39
CDS Hazard-Rate	2	487.2	27.5	40.5	18.4	89.0	0.39
CDS Negative-Exponential	1	486.7	22.8	35.2	15.4	80.5	0.42
CDS Uniform	1	485.9	24.6	38.9	17.7	85.4	0.39
MCDS (cluster size) Hazard-Rate	3	481.2	18.6	44.3	12.2	74.6	0.44
MCDS (time) Hazard-Rate	3	489.5	27.9	40.3	18.7	86.9	0.38
CDS Hazard-Rate (Beronono)	2		24.2	103.4	37.2	287.1	0.38
MCDS (cluster size) Hazard-Rate (Beronono)	3		24.9	107.1	61.3	158.2	0.32

Notes: # params: number of parameters; AICc: Akaike's Information Criterion corrected for small samples; ESW: Effective Strip Width; CV: Coefficient of Variation; MCDS: Multiple-Covariate Distance Sampling; Parenthesis: covariates tested. 1 – 4 analysis computed with CDS for pooled data; 5 – 6 analysis computed with MCDS for pooled data; 7 – 8 analysis computed for Beronono.

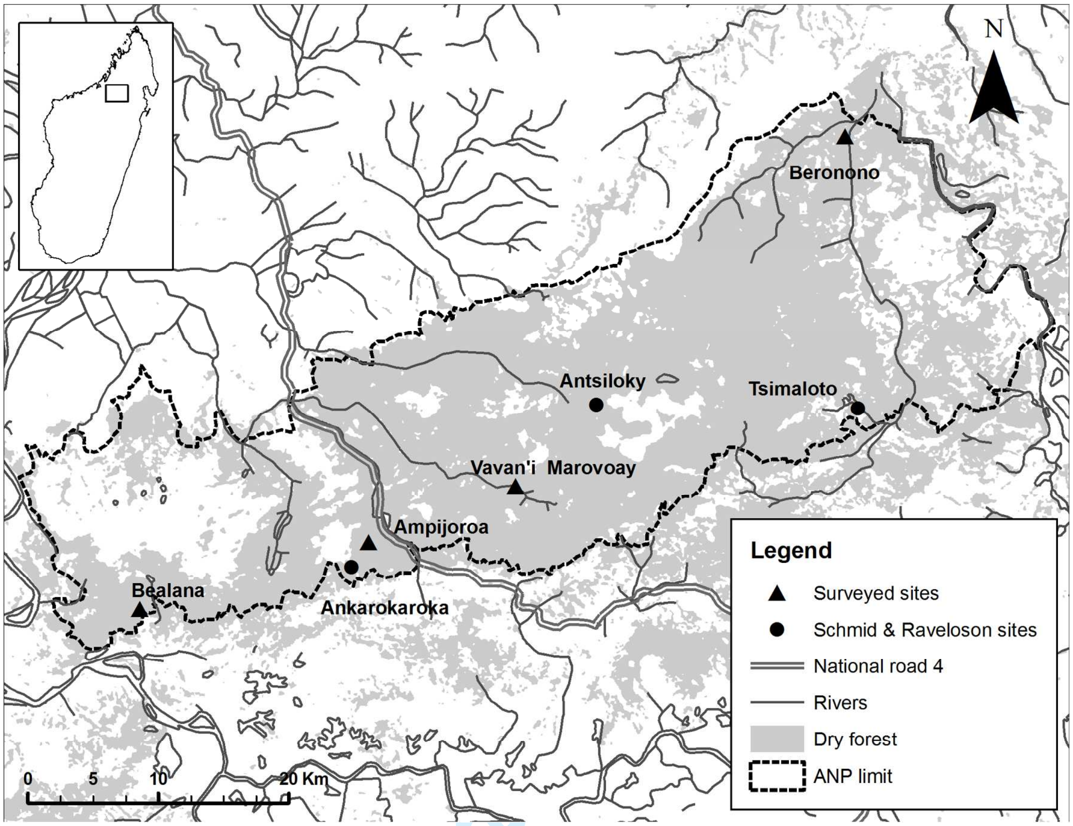

Figure 1. Map of Ankarafantsika National Park showing survey sites.

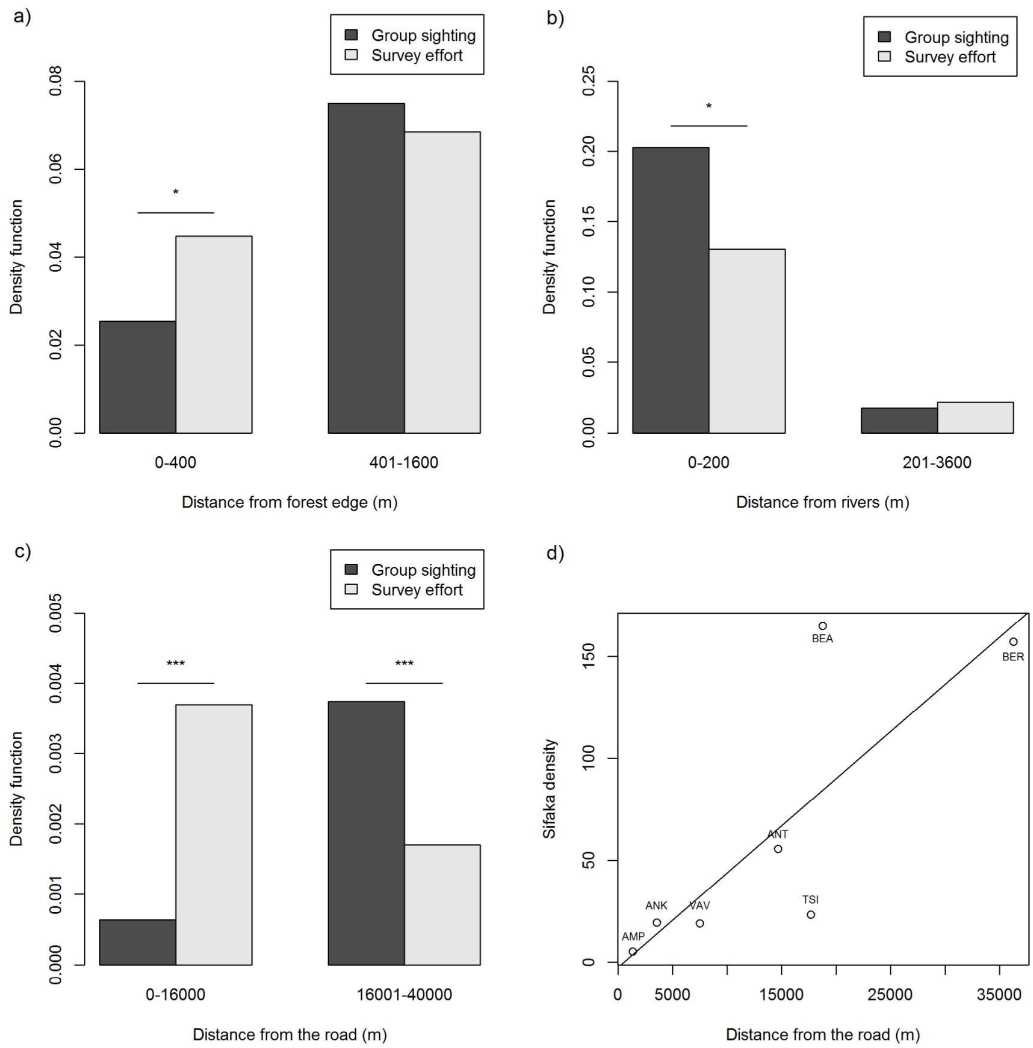

Figure 2. Effects of edges (a), rivers (b) and a national road (c and d) on sifaka density in Ankarafantsika National Park. Panels a to c: comparisons of distributions standardized by the uniform Kernel densities**;** Dark gray: *P. coquereli* group sightings distribution; light gray: survey effort distribution. Significant differences between distributions obtained using the Pearson's χ^2 Test for count data with 10,000 permutations are indicated with: * for p-values < 0.05; ** for p-values < 0.01; *** for p-values < 0.001. AMP – Ampijoroa; ANK – Ankarokaroka; VAV – Vavan'i Marovoay; ANT – Antsiloky; TSI – Tsimaloto; BEA – Bealana; BER – Beronono.