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Research Article

Spatial Variation in Density and Total Size Estimates in Fragmented Primate Populations: The Golden-Crowned Sifaka (*Propithecus tattersalli*)

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The golden-crowned sifaka (*Propithecus tattersalli*) is an endangered lemur species found only in the Daraina region, a very restricted area in north-eastern Madagascar. Its forest habitat is highly fragmented and expected to suffer from significant changes in the near future. The species is poorly known and only one census study, carried out in 2000, has ever been published. It is thus crucial to update the conservation status of the golden-crowned sifaka before major anthropogenic environmental changes take place. Using the line-transect approach, we estimated the species density in the main forest fragments located in both the peripheral and central parts of the distribution range, including both protected and unprotected areas. In parallel, we tried to determine whether an edge effect could be detected by comparing densities at different distances from the forest edges. We found important variation of sifaka densities among forest fragments. The total species abundance is thus difficult to determine, but we estimated that it is likely to be over 18,000, two to three times higher than previously thought. However, our data also suggested that most *P. tattersalli* live in forests located in the central part of the distribution range and that the estimated densities in the central part were high (>80 individuals/km^2). Two forest fragments, found to host a large part of the total population, are currently outside the managed area and their incorporation to the managed area is strongly recommended. Lastly, as expected for a folivorous and not heavily hunted species, our results are consistent with the hypothesis that this species does not experience a clear edge effect, at least during the first half of the dry season. This could be due to a high resiliency to habitat fragmentation or to the fact that fragmentation has been going on for some time. Am. J. Primatol. 71:1–9, 2009. © 2009 Wiley-Liss, Inc.

Key words: golden-crowned sifaka; *Propithecus tattersalli*; habitat fragmentation; abundance; edge effect

INTRODUCTION

Habitat loss and fragmentation are currently among the greatest threats faced by forest-dwelling species in many tropical regions of the world [Anderson et al., 2007; Harper et al., 2007; Q1 Mittermeier et al., 2006]. Primates are particularly affected because most of them are found within tropical forests, and over one in four species are either endangered or critically endangered because Q2 of environmental disturbances [IUCN, 2005]. The relationship between habitat degradation and changes in the spatial distribution and demography of primate populations is still poorly understood Q3 [Irwin, 2008]. One reason is that the process of forest fragmentation does not simply result in smaller versions of large forests [Fahrig, 2002]. Because small forest patches have a larger ratio of perimeter to area than large patches, the fragmentation process is characterized by an important increase of boundaries between forest and surrounding anthropogenic environment, potentially positively or negatively influencing forest-dwelling species [Debinski, 2006]. Edge habitats have transitional abiotic (e.g. lower

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level of humidity, increased wind speed, drier soils) and biotic (e.g. change in plant species composition) characteristics [Lehman, 2007]. Responses to edge effects are expected to be species-dependent and will depend particularly on whether or not the new transitional environment significantly reduces the access to feeding resources, as well as the connectivity between forest fragments [Anderson et al., 2007; Marsh, 2003].

Madagascar has suffered from drastic environmental changes in the last millennia and presents an extremely high level of forest loss and fragmentation [Ganzhorn et al., 2001; Harper et al., 2007; Smith, 1997]. Lemurs, which are endemic primates of Madagascar, are thus particularly affected by forest degradation and may be negatively affected by edge effects. Previous studies have demonstrated that the susceptibility of lemurs to these edge effects varies considerably among species [Ganzhorn et al., 2003; Irwin, 2007; Lehman, 2007; Lehman et al., 2006]. This variation has been suggested not only to depend mainly on their diet (folivorous *vs* frugivorous) [Lehman et al., 2006] and on their interaction with local human communities (e.g. hunting, taboos) [Jones et al., 2008], but also on their behavioural plasticity, i.e. their ability to adapt their diet and home range to their new environment [Deghan, 2003; Irwin, 2007; Wright, 2007]. Species-specific studies of spatial variation of densities among and within forest fragments are thuscrucial for understanding the impact of habitat fragmentation and to develop adequate conservation strategies.

Here, we studied the case of the golden-crowned or Tattersall's sifaka (*P. tattersalli*) [Simons, 1988] which is an endangered species of lemur only found in the Daraina region in north-eastern Madagascar (within the district of Vohemar, Fig. 1). *P. tattersalli* lives in one of the most restricted ranges of any lemur [Mittermeier et al., 2006] and its forest habitat is highly fragmented and surrounded by a matrix of agricultural areas, zebu cattle grazing savannas, and a network of riparian corridors [Vargas et al., 2002]. This species remains poorly studied mostly because of its narrow distribution in a relatively remote area, so much so that, soon after the species was scientifically described [Simons, 1988], the size of the total population was thought to consist of only 100 individuals [Anonymous, 1989]. The only demographic study to date, which allowed evaluating the golden-crowned sifaka conservation status, was carried out in 2000 [Vargas et al., 2002]. The authors collected data on the presence/absence of golden-crowned sifaka in nearly all fragments of the Daraina region. The total population size was estimated at 6,100–10,000 individuals based on density estimates performed in two forest patches located in a limited area near the main village of the Daraina region (Fig. 1). The method entailed recording observations at one or two hills for each patch. The golden-crowned sifaka distribution area, although not very large, includes surprisingly varied habitats. Moreover, the level of anthropogenic disturbances and edge effects, if any, may vary considerably depending on the proximity of human settlements or villages, and on the degree of exploitation of forest resources. It is, therefore, important to quantify the density of golden-crowned sifakas within different forest fragments located in central and peripheral parts of the distribution area, to obtain a better estimate of the total population size and its resiliency at the current level of habitat fragmentation.

The Daraina region is expected to suffer from anthropogenic changes in the near future with the pending tarring of the national road crossing the area and setting up of gold-mining companies. It is crucial to get an update on the conservation status of the golden-crowned sifaka before major environmental changes take place. Our goal was to estimate the golden-crowned sifaka density in five of the main forest fragments of this species range to (1) update our knowledge on the species abundance since the only study carried out in 2000, (2) assess the spatial variation of density among forest patches by increasing the number of surveyed forest patches and the intensity of these surveys and, finally, (3) determine whether an edge effect could be detected in this species during the period of the dry season surveyed (May–August).

METHODS

Population Densities and Total Species Abundance

To assess spatial heterogeneity in golden-crowned sifaka density among forest patches, we carried out line-transect surveys [Buckland et al., 2001; Marshall et al., 2008; Peres, 1999] in five of the main forest fragments spread throughout its distribution range [Vargas et al., 2002]: Ambohitsitondroina, located in the west of the Daraina region, Benanofy in the north-west, Antsaharaingy in the north-east, and Tsarahitsaka and Bekaraoka in the center, near the Daraina village (Fig. 1). The five surveyed fragments correspond to lowland dry deciduous forest and exhibit varied levels of human disturbance. Three fragments (Ambohitsitondroina, Antsaharaingy, Bekaraoka) are located within the ''Station Forestière à Usages Multiples'' (S.F.U.M. ''Multiple Usage Forest Station'') Loky-Manambato managed by the NGO Fanamby. The S.F.U.M. classification mandates protection of a biodiversity-rich area threatened by anthropogenic pressures, such as intensive wood and mining exploitation. Our census took place during the dry season in June to August 2006 and May to July 2008.

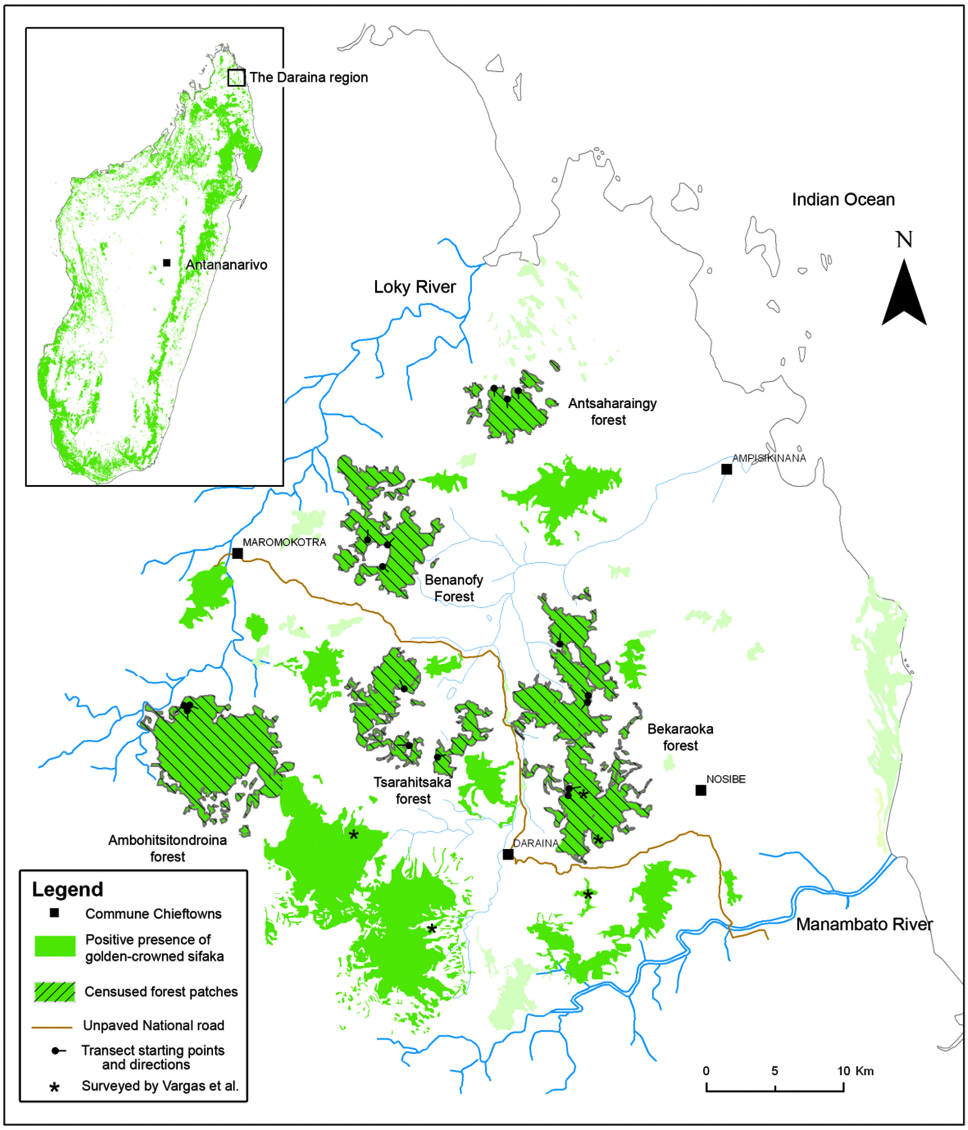

Fig. 1. Forest fragments surveyed. All forest fragments where *P. tattersalli* was shown to be present in the study of Vargas et al. (2002), are represented in grey. The fragments surveyed in this study are represented with diagonal lines crossing them. The approximate locations of the starting points and the direction of our surveys are represented by dots. The transects and corresponding ending points are not represented for the sake of clarity, but all GPS points are available upon request. The exact location of the sites censused by Vargas et al. (2002) was not available to us but, for comparison with our survey, stars have been added to the map to indicate the forest fragments that they surveyed.

For each surveyed forest patch, we randomly delineated between three and five line-transects regularly marked using flagging tape (20 line-transects in total). GPS coordinates for each flag were recorded only for the forest fragments surveyed in 2008 (14 line-transects). We tried to conduct transect lines from the edge to the interior of the different forest fragments avoiding existing trails and rivers that could bias abundance estimations [Peres, 1999] (Fig. 1). Because the forest habitat is highly fragmented, our survey effort varied between forest edges and centers (Fig. 2). The defined transects were between 1,300 m and 3,250 m. The altitude varied between 35 m (Antsaraharaingy) and 450 m (Benanofy) with most of the surveys conducted between 150 and 250 m. Transects were surveyed 6–10 times during 3–5 days by three 2-member teams to collect at least 40 observations as recommended by Peres [1999]. Every day, one team member changed team and transect to avoid observational biases among teams and to ensure that at least one team member had already walked that transect.

When a sifaka group was observed, the following data were collected: date, time, transect number, group size, and sighting distance and angle of the first animal seen (to compute perpendicular sighting distance). We used the sighting distance to the tree of the first animal seen as an estimate of the social

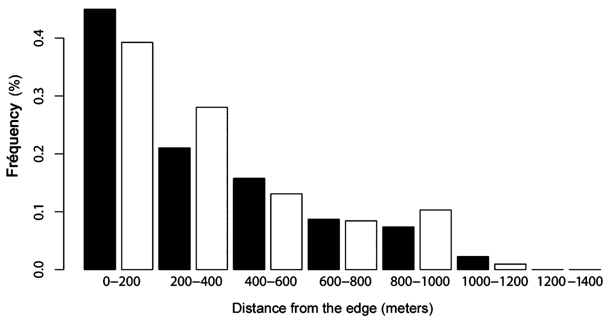

Fig. 2. Survey effort and group sightings. Black bars correspond to the distribution of the survey effort, as a function of distance from the edge (in meters). Many observations were made at distances < 600 m. White bars show the corresponding frequency distribution of the groups' sighting. The two distributions show similar shapes and are not significantly different.

group sighting distance. A number of studies have discussed the effect of group spread in the estimation of densities [Fashing & Cords, 2000; Marshall et al., 2008]. In particular, these authors have warned against the fact that ignoring spread may lead to overestimates of density for species whose groups spread out over large areas. However, in *P. tattersalli*, the mean group size is low (see results below) and individuals from the same group were located in the same tree at distances less than 5 m from each other in at least 80% of sightings. Also, by measuring the distance to the tree we were thus using a distance that was close to that of the center of the group. This effect is thus likely to be limited in our case. We then estimated sifaka densities (number of individuals per square km (ind/km^2)) in each prospected fragment using the distance sampling method [Buckland et al., 2001] as implemented in the DISTANCE 5.0 [Thomas et al., 2006]. In this approach, the survey area corresponded to the product of the total survey effort per fragment (km) by the effective sighting width (ESW) estimated by fitting a probability detection function to the histogram of perpendicular sighting distances. The hazard-rate model was used because it best fits the data for each forest patch. We noted that this model has generally had the best fit for primates [Plumptre & Reynolds, 1994], except for small samples [Whitesides et al., 1988]. To estimate the total species abundance, we multiplied the minimum and maximum density estimates by the area of occupancy. We computed the total species abundance using two different total occupancy areas: First, we used a total of 360 km^2, as in Vargas et al. [2002], excluding all habitats above 700 m because golden-crowned sifakas were not thought to be present above this altitude. Second, we used 440 km^2, the total forest habitat surface in the region [Vargas et al., 2002], because sifakas have recently been observed up to 1,000 m in the two evergreen mountainous forests (Antsahabe and Binara) [S. Wohlhauser, personal communication] suggesting that the available habitat may be larger than estimated by Vargas et al. [2002].

Sifaka Edge Effect Response

To assess whether sifakas experienced significant edge effects, we compared the number of sifaka groups encountered at different distances from the edge of the forest fragments surveyed in 2008 (Benanofy, Bekaraoka, and Antsaharaingy). Because animals may sleep in dense vegetation at night to avoid predation but forage in edge habitats during the day, the overall edge response could appear neutral when it actually contains negative (few hours before and after sleeping) and positive edge response (the rest of the day). We, thus, first checked if there was a variation in sampling intensity as a function of time of day by comparing the observed distributions of sighting frequencies between dusk/dawn (07.30–09.30 and 14.00–16.00) and the rest of the day (09.30–11.30 and 12.00–14.00) in the three surveyed fragments. Furthermore, the difference in sifakas' density between edge and the interior parts of a forest patch could also be caused by a higher animal detection probability in habitats with lower tree density [Lehman et al., 2006; Lehman, 2007]. We thus also checked whether there was a difference in the detection probabilities along transects by using a Spearman correlation test between perpendicular sighting distances and distances from the forest edge. We used a GIS analysis to estimate both our sampling intensity and the frequency of group encounters as a function of the distance from a fragment edge. To compute the distances from the edges for each sighting group, we first carried out a landscape classification using the ENVI software v.4.1 from a LandSat-7 Thematic Mapper imagery acquired in 2002. Forest patches were then digitized and the minimum distance between each social group sighting and the closest forest edge was computed using the ArcGIS software v.9.2. The distribution of these D distances is referred to as the observed distance distribution, D_{obs} ($D = 109$ corresponding to the total number of observations in Benanofy, Bekaraoka, and Antsaharaingy in 2008), to which a distribution of distances reflecting our survey effort could be compared. This second distribution was constructed by taking into account the fact that our survey effort varied between forest edges and centers. To do this, we first computed, for each of the geo-referenced flags mentioned above, the minimum distance from the edge by using the same procedure as above. Because some transects were surveyed more often than others, we weighted the distances correspondingly (e.g. the flags of a transect surveyed four times were repeated four times). We, thus, obtained a set of distances from the edge that was an unbiased representation of our sampling effort with regard to edge distance (D_{samp}). To test the edge effect, we compared the D_{obs} and D_{samp} distributions by using a Wilcoxon test. If there was no edge effect, we expected no difference between D_{obs} and D_{samp} distributions and higher encounter rates in areas where sampling intensity was higher. This study complies with the *American Journal of Primatology* requirements for the ethical treatment of animals, and was conducted in accordance with the CNRS guidelines and the laws of Madagascar and France.

RESULTS

Population Density and Size

In total, 306.8 km were surveyed and 205 social groups comprising 738 individuals were observed. The average size of the social groups was 3.6 (range: 2–8). Among the five surveyed forests, we were able to gather enough observations to compute density estimates for three forest fragments (Bekaraoka, Tsarahitsaka, and Benanofy) (Table 1). Indeed, we collected no observations for Ambohitsitondroina despite several days of census, and *P. tattersalli* were observed or heard only on a couple of occasions outside the survey period. Furthermore, only seven social groups corresponding to 19 individuals were observed in Antsaharaingy despite three days of census and a total of 27.9 km of survey effort. This limited number of observations (as a comparison, 60 groups, corresponding to 233 individuals were observed in Bekaraoka in 2008 for 55.4 km surveyed) did not allow us to compute accurately an ESW using the distance sampling method [Buckland et al., 2001; Peres, 1999]. Nevertheless, we decided to provide an estimate of sifaka density assuming that the ESW was the same as for Benanofy because observations were collected the same month by the same observers. Furthermore, the two forests, located next to each other, have similar characteristics. We observed lower ESW for the two censuses carried out in Tsarahitsaka and Bekaraoka in 2006 (13.5 and 11.3 m, respectively) than for the censuses made in 2008 (between 20.2 and 21.2 m). This discrepancy may result from a different ability to detect sifakas between the different teams in 2006 and 2008. However, the results obtained are clearly valid since we had census data in 2006 and 2008 for the same forest (Bekaraoka) and we obtained no significant differences (78 and 86 ind/km^2, respectively).

We also found important differences in sifaka densities among fragments with a value as low as 34 ind/km^2 for Antsaharaingy and as high as 90 ind/km^2 for Tsarahitsaka. Even excluding Antsaharaingy for which the number of observations was low, we still estimated a density of 55 ind/km^2 for Benanofy, which is 40 and 35% less than that of Tsarahitsaka or Bekaraoka, respectively.

Using the lowest density estimate (Antsaharaingy) and applying it to the available habitat assumed by Vargas et al. [2002] (360 km^2), we find an estimate of the total number of sifakas across the whole area of 12,240 ($\pm$3,960) individuals. If we use the largest value (Tsarahitsaka), we obtain 32,400 ($\pm$8,100) individuals. Given that Ambohitsitondroina seemed to harbor very low densities, we recomputed these numbers excluding this site (i.e. reducing the total area by 14% from 360 km^2 to 305 km^2) and found that the total abundance could be as low as 10,370 ($\pm$3,355) or as high as 27,511 ($\pm$6,862). If we take into account the forest habitat above 700 m and use an updated estimation of the occupancy area (440 km^2), we find that the total abundance could be as low as 14,960 ($\pm$4,840) or as high as 39,600 ($\pm$10,120), following the same reasoning as above. These values are necessarily extreme and unlikely to be correct because we are applying extreme densities even to fragments for which we have reasonable density estimates.

One way to obtain more reasonable estimates is to first focus on the four surveyed fragments where we were able to estimate the population size. Assuming for simplicity that we can add the estimates for these fragments (thus ignoring uncertainty on each estimate), we find that ~11,185 individuals are potentially living in these fragments. The total area of these forests corresponds to approximately 43% (163.5 km^2) of the total expected occupancy (excluding Ambohitsitondroina). Assuming that our survey was more or less representative of the golden-crowned sifaka habitat across the Daraina region, we could thus extrapolate this value to the total area and find a total of 26,011 individuals

TABLE 1. Density and population size across forest fragments

Forest fragment	Year	Surface (km^2)	♯ of observed individuals (groups)	Density (ind/km^2) and standard error	95% confidence intervals	Population size (standard error)	95% confidence intervals
Bekaraoka	2008	66.25	233 (60)	85.8 (0,23)	0.46–1.57	5,656 (1677)	3,072—10,414
Bekaraoka	2006	66.25	189 (53)	78.1 (0.23)	0.28–2.18	5,189 (1,575)	1,859—14,489
Benanofy	2008	56.65	160 (42)	55.4 (0,19)	0.19–1.60	3,142 (1,058)	1,084–9,107
Tsarahitsaka	2006	17.70	137 (43)	90.2 (0,23)	0.46–1.74	1,603 (400)	792–2,970
Antsaharaingy	2008	23.10	19 (7)	34.0 (0.11)*	NA	784 (232)*	NA

*These density population size estimates were computed by using the ESW for Benanofy (see text).

(excluding Ambohitsitondroina). We made a final calculation by applying to the nonsurveyed forests the lowest density estimated in this study and then adding the 11,185 individuals. This procedure gives a minimum population size of 18,733 individuals. These values should not be taken at face value; they represent currently the best available estimates for the *P. tattersalli* species abundance. The real number is likely to be between 11,000 and 26,000, and probably above 18,000.

Edge Effect

We found no difference between the sighting frequencies in dusk/dawn and in the rest of the day ($\chi^2 = 2.76$, df = 2, $P = 0.25$). Furthermore, we also found no significant correlation between the distance of the observer from the forest edge and the perpendicular detection distances ($r_s = 0.004$, $P = 0.45$). This result suggests that our ability to detect sifaka groups was not correlated to the distance of the observers to the nearest forest edge or to the time at which the observations were made. Regarding the density of animals at different distances from the edge, we were not able to detect any significant difference between D_{obs} and D_{samp} (Wilcoxon-test, P-value = 0.48), suggesting that if there is an edge effect it is limited or cannot be measured with our data discussed below.

DISCUSSION

Population Density and Size

With a total abundance ranging between 11,000 and 26,000 individuals, and probably above 18,000, our results strongly suggest that golden-crowned sifakas are more abundant than suggested by Vargas et al. [2002] who estimated a total size of 6,000 to 10,000 individuals. Although we remained cautious when extrapolating our density estimates to the whole Daraina region, we can be confident that our estimates are clearly higher than those previously obtained [Vargas et al., 2002]. Even if we limit ourselves to the four surveyed forest fragments, which represent approximately half of the available habitat for the species, we find a total of 11,185 individuals, which is higher than Vargas et al.'s [2002] highest estimate for the whole species. The density of *P. tattersalli* was shown to vary significantly among fragments in our surveys. The difference between our density estimates and those of Vargas et al. [2002] (i.e. between 17 and 28 ind/km^2) could thus be caused by the survey of different fragments with different densities extrapolated to the whole region. However, both Vargas's study and ours censused Bekaraoka, with a three-fold difference in density estimates. Furthermore, we surveyed this fragment in 2006 and 2008 and we found very similar and high values of estimated densities. A more likely explanation for the difference between studies is that different methods were used to estimate densities. Vargas et al. [2002] used a point counts method [Buckland et al., 2001] collecting sighted groups from hills and dividing the number of sightings by the total visible area. This method requires many replicates throughout the forest patch, particularly when low densities are estimated [Buckland et al., 2001; Kelley et al., 2007; Whitesides et al., 1988]. In their study, Vargas et al. [2002] only used one or two observation sites for each of the three forest patches (Fig. 1). Furthermore, because the individuals may be disturbed by the observer, the point counts method may lead to underestimating the density because of a deficit of sightings near the observer [Buckland et al., 2001]. Lastly, another factor that may explain their low density estimates is that the golden-crowned sifakas may not be easily seen from the hills where the observers are located because the sifakas often stay on the lower branches of the trees, at least during the dry season, when all the surveys were conducted, and when they were more easily detected from the ground [Personal Observation, 2006, 2008]. This suggests that the methods used by Vargas et al. [2002], widely used for songbird surveys, could be adapted for rapid census targeting initial conservation needs assessment, but the line-transects method may be more appropriate for more accurate primates census [see Hanya et al., 2003 for a counter-example]. We are confident that our estimates are not major overestimates since we found similar values in 2006 and 2008 for Bekaraoka, whoever was involved in the transect survey (EQ and local guides in 2006, AB, LC, JC, ER, and local guides in 2008).

If we exclude the case of *P. perrieri,* one of the most endangered primates of the world with a density of 3.11 ind/km^2 [Banks et al., 2007], the densities found for *P. tattersalli* are comparable to those estimated in related *Propithecus* species (Table 2). In Bekaraoka and Tsarahitsaka, the densities (85–90 ind/km^2) are particularly high, but this is not necessarily surprising given that *P. tattersalli* is less hunted than most other sifaka species, and these figures are lower than the highest values reported for *P. coronatus* (Table 2). Because the golden-crowned sifaka is a patchily-distributed species and lives in a very heterogeneous environment, its total size estimation is problematic. To provide the most accurate estimation possible, we tried in this study to capture the spatial heterogeneity in population density surveying forest patches both in (1) the peripheral part and in the center of the distribution range and (2) both in the protected or unprotected areas. We found a significant variability of density among forest patches with, for instance, a very low density of individuals for the large degraded forest patch Ambohitsitondroina (representing 15.2% of the total available distribution range). Such differences could be due to habitat

TABLE 2. Density estimates for *Propithecus* species

Species name	Density (ind/km^2)	Study site	Reference
P. tattersalli	34–90	Daraina	This study
P. perrieri	3.1	Analamerana	Banks et al. [2007]
P. edwardsii	7.6	Ranomafana	Irwin et al. [2005]
P.verreauxi	49	Antserananomby	Kelley et al. [2007]
P. coquereli	60	Ankarafantsika	Ganzhorn [1988]
P.coronatus	48–173	Anjamena	Muller et al. [2000]

differences, feeding resource availability in relation to the census season. But we were not able to test these hypotheses in this study. A low census estimate of 11,185 is provided by the forest fragments surveyed, and an upper bound of 26,011 is probably reasonable, but the extrapolation to the whole Daraina region should be regarded as tentative. To refine this estimate, new census should be conducted using the same methodology in the forest types that could not be censused in 2006 and 2008, namely Ampondrabe and Bobankora.

Golden-Crowned Sifaka Edge Effect Response in Dry Season

We found no significant difference between the densities of *P. tattersalli* at different distances from the edge. This result is consistent with the hypothesis that this taxon does not experience edge effects (i.e. neutral response), but it should be interpreted with caution. Indeed, this effect may occur because this species is largely folivorous during the dry season [Irwin, 2006; Meyers, 1993; Personal Observation, 2006, 2008], the period during which our surveys took place, and the abundance and the quality of leaves seem to be less influenced by edge effects than those of fruit [Lehman, 2007; Norconk & Grafton, 2003]. A neutral edge effect response has been already observed in other folivorous lemurs species that were not hunted [Lehman et al 2006; Lehman, 2007]. Another factor that could explain our result is that golden-crowned sifakas, protected by local taboos, are thus not hunted by local populations. Hunting appears to have been important in the 1990s, in some of the forest fragments at least, because of a large number of itinerant gold miners who did not always follow local taboos [Meyers & Ratsirarson, 1989]. Mining has significantly decreased in the past few years, however, and we found large *P. tattersalli* densities near Andranotsimaty, one of the main gold mining villages of the region. Probably because mining here is performed by local people and at a small scale.

Conclusion and Conservation Implications

Altogether, our results suggest that there are more *P. tattersalli* individuals within the Daraina region than was thought. Although the exact number of golden-crowned sifakas is difficult to estimate with certainty, it seems reasonable to state that this number is probably between 11,000 and 26,000, perhaps averaging above 18,000 individuals. Although this number is higher than originally expected, it is important to note that this species is far from being safe. The golden-crowned sifaka distribution range is one of the smallest of any lemur [Mittermeier et al., 2006], and our data suggest that perhaps half of the individuals are concentrated in the center of the Daraina region (Bekaraoka and Tsarahitsaka) and in Benanofy. Neither Tsarahitsaka nor Benanofy are currently within the S.F.U.M and our results strongly suggest that these two forest fragments should be protected as quickly as possible. The possible neutral edge response uncovered for *P. tattersalli* in this study, combined with the fact that this species is known to have a very flexible feeding behaviour [Meyers, 1993], suggests that golden-crowned sifakas have a relatively good resilience to habitat fragmentation. As we noted above, however, our surveys were conducted between May and August corresponding to most of the dry season. Golden-crowned sifaka mating and male dispersal occur during the rainy season (approximately January to May) when individuals mainly feed on fruits [Meyers, 1993], which are often more abundant in interior habitats [Deghan, 2003; Wright, 2007]. It might thus be important to determine whether similar densities would be observed and whether edge effects could be detected during the rainy season. Similarly, density estimates performed at the end of the dry season (September/October), when the feeding resources become scarcer within the forests, would also be critical.

One further point to keep in mind is that it is now difficult to encounter very large forest fragments (>5000 ha) in the Daraina region, and an alternative explanation for our ‘‘neutral’’ edge effect might be that there are no sufficiently large forests left for us to find samples that could be far enough from the edges for us and to which we could actually compare edges. Here, more comparative work would be necessary on other *Propithecus* species living in regions where there still are large forest fragments or on smaller species, such as *Microcebus*, living in the Daraina region. For these species, the heart of the largest fragments may be far enough from the edge so as to allow the detection of edge effects.

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