

RESEARCH ARTICLE

Lemurs in a Complex Landscape: Mapping Species Density in Subtropical Dry Forests of Southwestern Madagascar Using Data at Multiple Levels

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The study of southern dry forest lemurs has been largely restricted to small reserves; yet, the majority of the region's lemur populations reside outside protected areas. *Lemur catta* and *Propithecus verreauxi* occupy the same forests but have different dietary preferences. This study assessed *L. catta* and *P. verreauxi* population densities across a 3-km dry forest gradient (1,539 ha) in southern Madagascar. The study was designed to allow lemur densities to be related to particular forest types. A particular aim of this study was to collect lemur data in both protected and unprotected areas. Density estimates were calculated using point transect distance sampling in a study area that contained the Beza Mahafaly Special Reserve and the adjacent disturbed forests. The highest densities recorded for each species were in the protected area where the two species were most segregated in their distribution, with *L. catta* density highest in gallery forest type and *P. verreauxi* density highest in dry deciduous. Densities of both species varied widely outside the protected area, but *P. verreauxi* density was more uniform than was *L. catta*. Results of this study indicate that patterns of lemur density in protected areas are not representative of patterns in disturbed forests; this also suggests that we cannot fully understand the ecological constraints facing primate species by studying them only in protected areas. This research highlights the value of pairing the study of landscape-level patterns of species distribution with both local ground-level ecological interpretations and broad-scale satellite data; information from only one level may give an incomplete view of the community. *Am. J. Primatol.* 73:38–52, 2011. © 2010 Wiley-Liss, Inc.

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INTRODUCTION

Madagascar is biogeographically diverse with a host of vegetation types supporting a rich lemur fauna. Forest loss in Madagascar is ubiquitous in all forest types, but fortunately, the rain forest and the western dry forest lemur species enjoy protection in an array of reserves—both small and large—throughout their respective biogeographic regions. Despite the high plant endemism of southwestern Madagascar [Phillipson, 1996], this region has a dearth of protected areas compared with other biogeographical regions in the country [Hannah et al., 2002; Moat & Smith, 2007]; its endangered subtropical dry forests have received comparably little consideration for lemur conservation, despite the fact that dry and spiny forest loss rates are equal to, or even higher than, Malagasy rain forests [Harper et al., 2008; Mittermeier et al., 1994].

Since President Marc Ravalomanana's 2003 announcement to triple the country's protected areas, the Malagasy Government has created 15 new protected areas [Lovgren, 2007], including six new parks [Madagascar National Parks; Norris,

2006]. Two protected areas in southwestern Madagascar have been extended in size, including Tsimanampetse National Park [Bradt, 2007] and Beza Mahafaly Special Reserve (BMSR) [Raharimalala, 2008], and a couple of community-managed protected areas have been newly designated [Ministère de l'Environnement et des Forêts], but even with these additions, southwestern Madagascar still lags behind other regions in percent forest protected—less than 5% of southwestern dry deciduous and

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spiny forest vs. nearly 40% for humid forest [Moat & Smith, 2007].

As the only two diurnal lemurs in Madagascar's southern forests, ring-tailed lemur (*Lemur catta*) and Verreaux's sifaka (*Propithecus verreauxi*) are the region's flagship species [Durbin, 1999; Jolly, 2003b; Walpole & Leader-Williams, 2002]—charismatic symbols of the ecosystem that serve to stimulate conservation awareness in the region [Hawksworth et al., 1995; Simberloff, 1998]. Both taxa are endemic to southern Madagascar [Mittermeier et al., 2006], and while their geographic ranges overlap, there are significant gaps in our knowledge of their respective distributions. With so little of this region's forests protected, a large proportion of the two species' populations must, therefore, live in unprotected forests.

L. catta is a fairly large lemur (2.3–3.5 kg) living in female-dominated groups of 6–24 animals with an average group size in protected subtropical dry forests of 11.5–16 noninfants [Gould et al., 2003; Jolly et al., 2002; Sussman, 1991]. It is the most terrestrial of all lemurs [Goodman et al., 2006], spending a considerable proportion of its time travelling and feeding on the ground, especially during the dry season. *L. catta* is largely herbivorous, consuming a varied diet of fruits, leaves, herbs, and flowers, depending on resource availability [Sauther et al., 1999]. *Tamarindus indica* is an important food source for *L. catta*, because it is the only species it feeds on throughout the year [Simmen et al., 2006].

At 3–3.5 kg, *P. verreauxi* is one of the smaller sifakas. It, too, lives in female-dominated groups, although they are typically smaller than those of *L. catta* (range: 2–14 individuals [Richard et al., 2002]). Even though it is a vertical climber and leaper, it also descends to the ground to travel and feed. This sifaka species is highly folivorous and includes a higher diversity of plant species in its diet than does *L. catta* [Simmen et al., 2003; Yamashita, 2002].

The dry forests of inland southern Madagascar consist of three forest types: gallery (or riverine), dry deciduous, and spiny. When all three forest types are found in a single landscape, these forests are typically arranged along a moisture gradient with gallery located along river courses, spiny situated most distant from the river, and dry deciduous positioned in between. Both lemur species are known to utilize all three forest types to some extent. Efforts to implement conservation measures for the two lemur species are hampered by both an absence of forest classification maps representing the diversity of vegetation types at local and landscape-level scales, and a lack of understanding of how lemurs utilize multiple forest types.

There have been a host of mapping projects in Madagascar [Du Puy & Moat, 2003; IEFN, 1996; Mayaux et al., 2000; Nelson & Horning, 1993], but

the latest national mapping effort, known as the Vegetation Atlas of Madagascar [Moat & Smith, 2007], may be the most promising for conservation planners. The Critical Ecosystem Partnership Fund Madagascar Vegetation Mapping Project produced an updated vegetation map with a working scale of 1:250,000 and 15 mappable vegetation units [Moat & Smith, 2007]. Despite their obvious value in some environmental applications, national maps such as this do have limitations, especially for applications at the landscape (100–1,500 ha), watershed (1,000s of hectares), or even the ecoregional (10,000s of hectares) scales where differentiation between forest classes and spatial resolution is of great importance. This is especially true for dry forests which consist of a number of different forest classes which may not be differentiated on broader scale maps. In the case of the Vegetation Atlas of Madagascar, users are not able to distinguish either between the southern spiny and dry deciduous forest or the wooded bushland mosaic and gallery forest [Moat & Smith, 2007].

Both lemurs are well studied in the protected forests of BMSR and Berenty Private Reserve [Brockman et al., 2001; Gould et al., 1999, 2003; Richard et al., 2002; Sauther et al., 1999; Sussman, 1991; Yamashita, 2002], but there are still comparably few studies on lemur populations inhabiting forested areas outside these small, roughly 100 ha protected parcels of the mixed dry deciduous and gallery forest. Consequently, our current understanding of both *L. catta* and *P. verreauxi* is based primarily on studies conducted in the protected gallery forests, which experience minimal anthropogenic impacts [Gould et al., 2003; Jolly & Pride, 1999; Jolly et al., 2002; Richard et al., 1993]. Still, the vast majority of forests in the southwest are at risk of degradation from such threats as livestock grazing, fuelwood collection, agricultural conversion, and mining activities [Fenn, 2003; Sussman & Rakotozafy, 1994].

Simultaneous sampling of the two sympatric lemur species has been rare, apart from Berenty Reserve where both lemurs have been censused at sporadic intervals since the early 1960s [Jolly, 1972; Jolly & Pride, 1999; Norscia & Palagi, 2008]. Simultaneous sampling took place in 1970, when Jolly [1972] recensused both species in a 10 ha study area of the gallery forest; however, no comparisons were made between densities of the two species. Presumably the data are statistically comparable, but the intent of the study was to assess changes in troop size and troop spacing behavior. In 1981, both species were censused in the Malaza portion (94 ha) of Berenty Reserve. Multiple researchers used both spot check and continuous count methods until consistent troop numbers and composition were reached; however, only that fraction of the *P. verreauxi* population ranging along forest paths could be recorded because animals were skittish. In

addition, researchers noted that the accuracy of the counts may have been affected by differences in lemur detectability by vegetation type [Howarth et al., 1986]. These studies illustrate some of the difficulties in making inferences about lemur density in areas consisting of multiple vegetation types. Surveys in small areas characterized by a single forest type, may not be representative of populations in other areas of the same forest type. And, unless one can be sure that a complete census has been achieved, differences in detectability should be accounted for. The sampling design used in the Berenty studies, discussed above, limits the ability to make statistically significant species density comparisons by habitat. Furthermore, we are precluded from comparing density estimates obtained in single species studies because they were obtained using a variety of sampling methods, at different times of the year, and often in different locations (typically in different reserves). Consequently, the vast majority of published density estimates for both lemur species do not extend beyond protected, and largely habituated, populations [Brockman et al., 2001; Gould et al., 2003; Jolly & Pride, 1999; Koyama et al., 2001; Merti-Millhollen et al., 2003; Richard et al., 1991; Simmen et al., 2003; Sussman, 1991; Yamashita, 2002].

Here, we provide a comparative study of the spatial distribution of *L. catta* and *P. verreauxi* in three forest types in and around the BMSR. This study combines a landscape-level model of species density and distribution with both fine-scale ecological forest observations and broad-scale satellite spectral data, in order to elucidate patterns that may otherwise be obscured at just a single level [Maurer, 1999]. The study area was classified by vegetation type, and lemur density was estimated during

the dry season using distance sampling methods [Buckland et al., 2001]. Lemur density was then compared by species, protection status, and forest type. Studies, such as this, are vital to conservation planning efforts, as effective conservation planning depends on availability of data about populations living in varied habitats.

METHODS

Study Area

The 1,539-ha study area includes both the 600 ha BMSR as well as the surrounding unprotected forested lands (Fig. 1). The entire reserve is embedded in a human-dominated landscape with human activities taking place both outside and within. The reserve (44°37' East, 23°39' South) is located in southwestern Madagascar, 35 km north-east of Betioky Sud, and it consists of two discontinuous parcels (Fig. 1). Forest structure and composition vary by soil moisture and soil type, with taller trees occupying the wetter soils closer to the Sakamena River and denser stands of shorter trees found on drier soils [Lowry et al., 1997; Sussman & Ratsirarson, 2006]. The most common plant species found in the gallery forest are *T. indica* (Fabaceae), *Quisivianthe papinae* (Meliaceae), and *Tarenna pruinosa* (Rubiaceae), whereas the main plant species found in the dry deciduous forest are *Acacia bellula* (Fabaceae), *Salvadora angustifolia* (Salvadoraceae), *Euphorbia tirucalli* (Euphorbiaceae), and trees in the genus *Grewia* (Malvaceae). The spiny forest is dominated by *Alluaudia procera*—of the endemic family, Didieriaceae—*Commiphora* sp. (Burseraceae), *Gyrocarpus americanus* (Hernandiaceae),

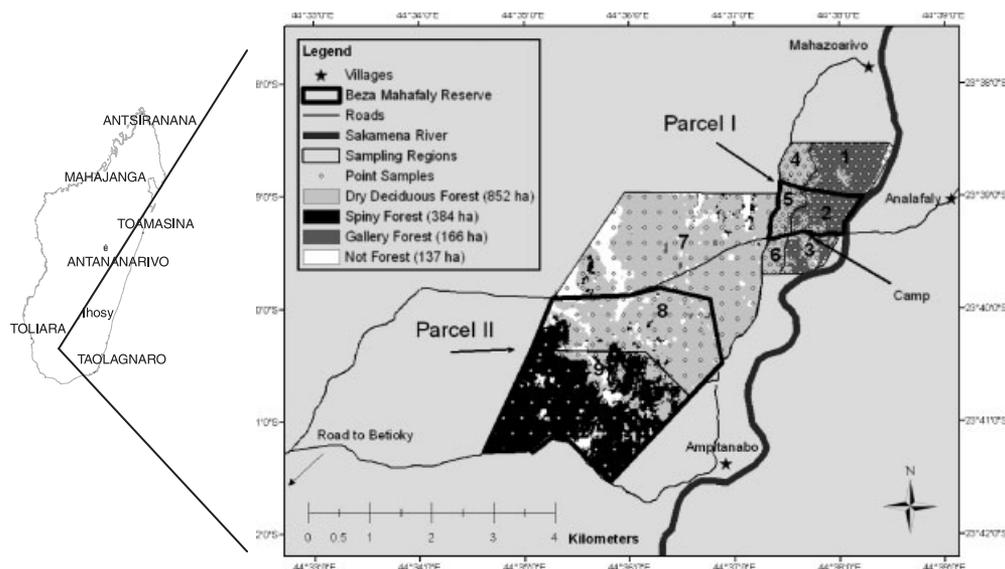


Fig. 1. Study area shown with forest classification derived from a random forest classifier and sampling regions overlaid on point samples.

Cedrelopsis grevei (Ptaeroxylaceae), and *E. tirucallii* (Eurphorbiaceae).

At 80 ha, Parcel I is the smaller of the two, and it is the site where most studies have been conducted [e.g., see Sussman & Ratsirarson, 2006 for a summary of earlier studies] (Fig. 1). A barbed-wire fence was erected in 1979 (and underwent repairs in 2007) and trails were cut thereafter creating a network of approximately 100 m square plots [Sussman & Ratsirarson, 2006]. Before the construction of the fence, this parcel was utilized by local residents and their livestock. This parcel comprises both gallery and dry deciduous forest. Unprotected forests immediately adjacent to Parcel I have a similar forest composition, and are still utilized by local people, and are degraded to varying degrees. Parcel II, at 520 ha, is situated from 0.5 to 4 km west of the Sakamena River and consists largely of dry deciduous and spiny forests, although it is dominated by spiny vegetation (Fig. 1). Human activities in Parcel II (sanctioned and otherwise) include agriculture, fuelwood collection, lumber collection, tree lopping, tree chopping, and livestock grazing. Reserve staff sporadically patrolled the southern-most end of Parcel II for illegal cutting of *A. procera*; otherwise, on the ground, there was little difference in land use activities outside the reserve and inside Parcel II. In order to discern differences in lemur density between areas closed to human activities and those open to human activities, Parcel I was identified as the only “protected area” in this article, although in reality both Parcels make up the formal protected area.

The land cover of the study area was classified into four types (gallery forest, dry deciduous forest, spiny forest, and not forest), using a classification algorithm that analyzed multi-temporal satellite imagery [Axel, 2010]. Tropical dry forest landscapes can be challenging to classify because their numerous vegetation types have similar spectral properties [Sanchez-Azofeifa et al., 2003]. Nonparametric decision trees are well-suited for such complex ecological classification problems [De’ath & Fabricius, 2000; Hansen et al., 1996], and in recent years, their use has increased in land cover mapping, particularly at broad mapping scales [Friedl & Brodley, 1997; Hansen et al., 1996, 2000; Xu et al., 2005].

The classification algorithm used to implement a decision tree-based classification of the landscape was a “random forest” approach. The procedure generates a large number of classification trees by using subsets of the entire data set. It then chooses the forest type that is most often selected by the model for each data point, as the forest type that best describes that data point. Further details on the classification are described in [Axel, 2010]. For a detailed description of random forest, the reader is referred to the manual (http://oz.berkeley.edu/~breiman/RandomForests/cc_home.htm) or Breiman [2001].

As calculated from the classified image, the study area (BMSR and surrounding area) consisted mostly of dry deciduous forest (55%), followed by spiny forest (25%), gallery forest (11%), and non-forest (9%) (Fig. 1). The largest area of intact (undisturbed and unbroken) forest was found in Parcel I. Parcel II contained the majority of spiny forest in the study area. Dry deciduous and spiny forests dominated the western half of the study area; the majority of nonforested lands were found there, as well. Nonforested lands consisted of either bare soil, grasslands, woodlands with sparse tree cover, bushland, and/or agricultural fields.

Field Measurements

The study area was divided into nine sampling regions based on reserve boundaries, roads, and forest types (Fig. 1). Sampling regions ranged in area from 19 to 528 ha, with smaller areas in and around Parcel I and the rest in and around Parcel II. A triangular point array sampling grid of 404 points, with a random start location, was overlaid on a map of the study area (Fig. 1) to identify locations where lemur counts were to be made. The distances between points on the grid varied between 115 m in the gallery forest and 300 m in the spiny forest, with sampling points placed in proportion to lemur density (i.e., more samples in areas believed to have higher density) to reduce variance and confidence intervals of the final estimate [Strindberg et al., 2004].

Distance sampling was chosen as the estimation method, because it is a method which can account for differences in lemur detectability owing to such factors as habitat type, weather condition, observer, etc. [Buckland et al., 2001]. The distance from each sampling point to the lemur group was recorded and used to estimate the “detection function,” which describes the probability of detecting a lemur group as a function of distance from the observer. Reliable estimates of abundance and density from distance sampling depend on meeting the conditions of three assumptions: (1) all individuals at the sampling point are detected; (2) all individuals are detected at their initial location (e.g., no evasive movements before detection); and (3) all distances are measured accurately [Buckland et al., 2001]. Sampling methods were designed to meet these assumptions.

Distance sampling can be performed using either line or point transects (sensu [Buckland et al., 2001]); point sampling was chosen because it has an advantage over line transect sampling when sampling for multiple species in patchy habitats, especially when habitat data are also being collected [Buckland et al., 2001]. In addition, point sampling allows more time for observers to detect and locate animals and this can be advantageous when sampling arboreal groups that may be feeding or

sleeping; point samples were especially useful in the dry season as many groups were detected when the observers heard lemurs feeding in the dry vegetation. Point samples are independent sampling units when they are systematically spaced, such that spacing between lines of points is equal to spacing between successive points along lines; points established along transect lines in which points are not evenly spaced across a region are a form of cluster sampling [Strindberg et al., 2004].

Both *L. catta* and *P. verreauxi* are social primates; therefore, data were collected on lemur groups rather than on individuals, in order to meet the assumption of sighting independence. Double-counting of moving groups is not problematic when using point samples provided that detections are independent of each other (i.e., animals are not “herded” by observers to subsequent points). Repeated observations of the same group (i.e., double-counting) will not violate the assumption of independence, so long as groups are not detected more than once from the same point [Rosenstock et al., 2002]. In the case of lemurs, this is easy to ensure.

Point samples used to estimate lemur density were sampled twice, once during the period June–July 2006, and again during June–August 2007. Each point sample equals a single unit of effort. Sampling was conducted during the dry season when detectability of lemurs was improved by some tree species being in leaf-off condition [Ratsirarson et al., 2001], and by the ability to hear lemurs moving through and feeding on dry vegetation. All sampling was conducted between 08:00 and 11:30 h and between 13:00 and 16:30 h, at times without rain or excessive wind. All point samples were accessed on foot and approximately 10 points were sampled per day. Each day was divided into two sampling sessions, morning and afternoon. On a little more than half the days, we sampled within the same region during both sessions. Within each sampling session, we typically sampled a set of points within the same area of the region. Time between sampling points varied according to distance between points and presence of lemur groups, but generally, 30 min passed between point samples.

Observers were trained in the method and all worked together at each sampling location. Each of the four observers in the team played a specific role in lemur sampling. I collected locations of the lemur groups using a Global Positioning System (GPS) and served as recorder of all information, whereas another was responsible for collecting distances with the laser range finder. Meanwhile, the two other members of the team counted the number of individuals in the group; if the group fled before all members were counted, they followed the group to obtain the group size.

On arrival at the point sample, observers waited approximately 2 min before beginning the 5-min

sampling period. Counts of all individuals in each lemur group (known as clusters in distance sampling sensu [Buckland et al., 2001]) were conducted for 5 min at each sampling point; infants born in the sampling season were not included in group counts. On rare occasions, multiple groups of a single species were detected from the same point, but individuals of each group were easily differentiated owing to distance between them, except in two cases. These instances involved altercations between groups, and in each case, groups were followed after they dispersed and individuals of each were counted. To the best of our knowledge, groups represent social groups.

Observations from 2006 and 2007 were pooled for analysis. Detection distances (required to model the detection function under the distance sampling methodology) were estimated for all observations using one of two methods: (1) when groups could be visualized from the sampling location, the horizontal distance to the group was determined using a laser range finder, and (2) in those cases where the group was heard but not seen from the sampling location, the group was located and its coordinates were recorded using a Garmin V GPS fitted with a Titan III external antenna (GPS Outfitters, Inc., Stephens City, VA), and external antenna (GPS Outfitters Titan III) and detection distances were later calculated in a geographic information system using ArcView 3.2 [Environmental Systems Research Incorporated, Redlands, CA].

Lemur Groups

Group size detected per point sample was mapped where lemurs were detected. If lemurs were detected at a sampling point in both field seasons, group size was averaged. Unequal variance *t*-tests [Ruxton, 2006] were used to test for differences in group size between species, as well as for differences in group size of each species by forest type (for dry deciduous vs. gallery forest only, as too few lemur groups were sighted from spiny forest sampling points to include all three forest types in this comparison). Each data point represents a sighting of a single group.

Lemur Density Estimates Within Mixed-Forest Sampling Regions

Given that very few large patches of any single forest type remain in the study area, it is useful to examine the patterns of species distribution by mixed-forest regions. Lemur density was estimated in sampling regions comprising multiple forest types in order to make comparisons between specific areas in the study area.

To estimate lemur density, first a detection function was fit to the observed distances between observer and lemur group (i.e., the distance between

observer at the sample point location and the lemur group location). The proportion of lemurs missed on the survey within the truncation distance (i.e., the distance beyond which data were excluded from analysis) can then be estimated; this represents the probability of detection p . Lastly, the estimate of lemur density is adjusted (upwards) for p to account for the proportion of the population that was undetected at the point samples. For a good overview of the method see Thomas et al. [2002], and for details of its use and analysis consult Buckland et al. [2001].

Density and probability of detection were estimated using the computer software DISTANCE 5.0 [Thomas et al., 2006]. One-way analysis of variance tests were used to test for differences in distance-to-groups (i.e., lemur detectability) by species, habitat, time of day, year, and group size. Final models were selected using Akaike's Information Criterion (AIC) [Burnham & Anderson, 2002]. Paired-tests for differences by sampling area in density, both between and within, lemur species were performed using a Z -test approximation of Sattthewaithe's Approximation [Thomas et al., 2006].

Lemur Plot Density Estimates Within Forest Types

In order to compare lemur density by forest type, estimates of lemur density were also calculated for the dry deciduous and gallery forest types, as shown in Figure 1 (there were insufficient data to calculate density for spiny forest). Here, it was necessary to calculate a single "plot density" for each sampling point because points were located in sampling regions characterized by multiple forest types. In this context, "plot density" was defined as lemur abundance per area forest type. To calculate lemur abundance, lemur counts at each point sample were adjusted for probability of detection. Plot area was then calculated by dividing the area of each forest type by the number of sampling points located within it. Lemur abundance was then divided by plot area to calculate lemur plot density. To calculate biomass/hectare, biomass of *L. catta* was based on average adult weight at BMSR of 2.211 kg [Sussman, 1991] and biomass of *P. verreauxi* was based on average adult weight at BMSR of 2.8 kg [Richard et al., 2000].

Tests for differences in plot densities of lemur species among different forest types, as well as between protected and unprotected parts of the study area, were performed using three generalized linear models to account for an overabundance of zeros in the data and the resulting overdispersion (i.e., a higher than expected variance). The three candidate models identified included: (1) a simple negative binomial model (NB) with a log link function, (2) a zero-inflated Poisson model (ZIP), and (3) a zero-inflated negative binomial model (ZINB) [Martin et al., 2005; Potts & Elith, 2006;

Sileshi, 2008]. Vuong tests and likelihood ratio tests were used to select the best candidate model [Vuong, 1989]. All models were fit in R using the zeroinfl() function from the pscl package [R Development Core Team, 2008; Zeileis et al., 2007].

This research complied with protocols approved by Michigan State University Institutional Animal Care and Use Committee, adhered to the legal requirements of Madagascar's Association Nationale pour la Gestation et Aires Protégées, and was conducted in compliance with the American Society of Primatologists' Principles for the Ethical Treatment of non Human Primates.

RESULTS

Lemur Groups

There were nearly twice as many *P. verreauxi* group detections ($n = 102$) as there were *L. catta* group detections ($n = 56$), but *L. catta* groups were significantly larger than those of *P. verreauxi* ($t = 08.16$, $P < 0.001$, $df = 80$) (Table I, Fig. 2A, B). Mean group size of *L. catta* was 9.5 lemurs, and there was no significant difference in mean group size between the gallery (8.99) and dry deciduous forest (10.36) ($t = 1.46$, $P = 0.15$, $df = 39$) (Table I). However, the majority of largest *L. catta* groups (71%), 13–20 animals, were detected outside the reserve in the dry deciduous forest of Region 7. Of the 9 *L. catta* groups in Region 7, 5 contained greater than the average *L. catta* group size of ≥ 13 animals sensu [Gould et al., 2003]. In contrast, only 2 of the 45 groups in Regions 1–6 contained ≥ 13 animals. Mean group size of *P. verreauxi* was 5.44 lemurs, and group size was significantly higher in the dry deciduous forest (5.71) than in the gallery forest (4.87) ($t = 1.98$, $P = 0.05$, $df = 95$) (Table I). The distribution of *L. catta* in the study area was more restricted and clustered than that of *P. verreauxi*; *L. catta* groups were more clustered in the interior portion of the protected gallery forest (Fig. 2A, B).

Lemur Density Estimates Within Mixed-Forest Regions

Lemur detectability varied by both species and habitat, but there was no difference in lemur

TABLE I. Comparison of *L. catta* and *P. verreauxi* Groups

Group size	<i>L. catta</i>	<i>P. verreauxi</i>
Number	56	102
Minimum	2	1
Maximum	20	11
Mean	9.50	5.44
Standard deviation	3.37	2.18
Gallery forest	8.99	4.87
Dry forest	10.36	5.71

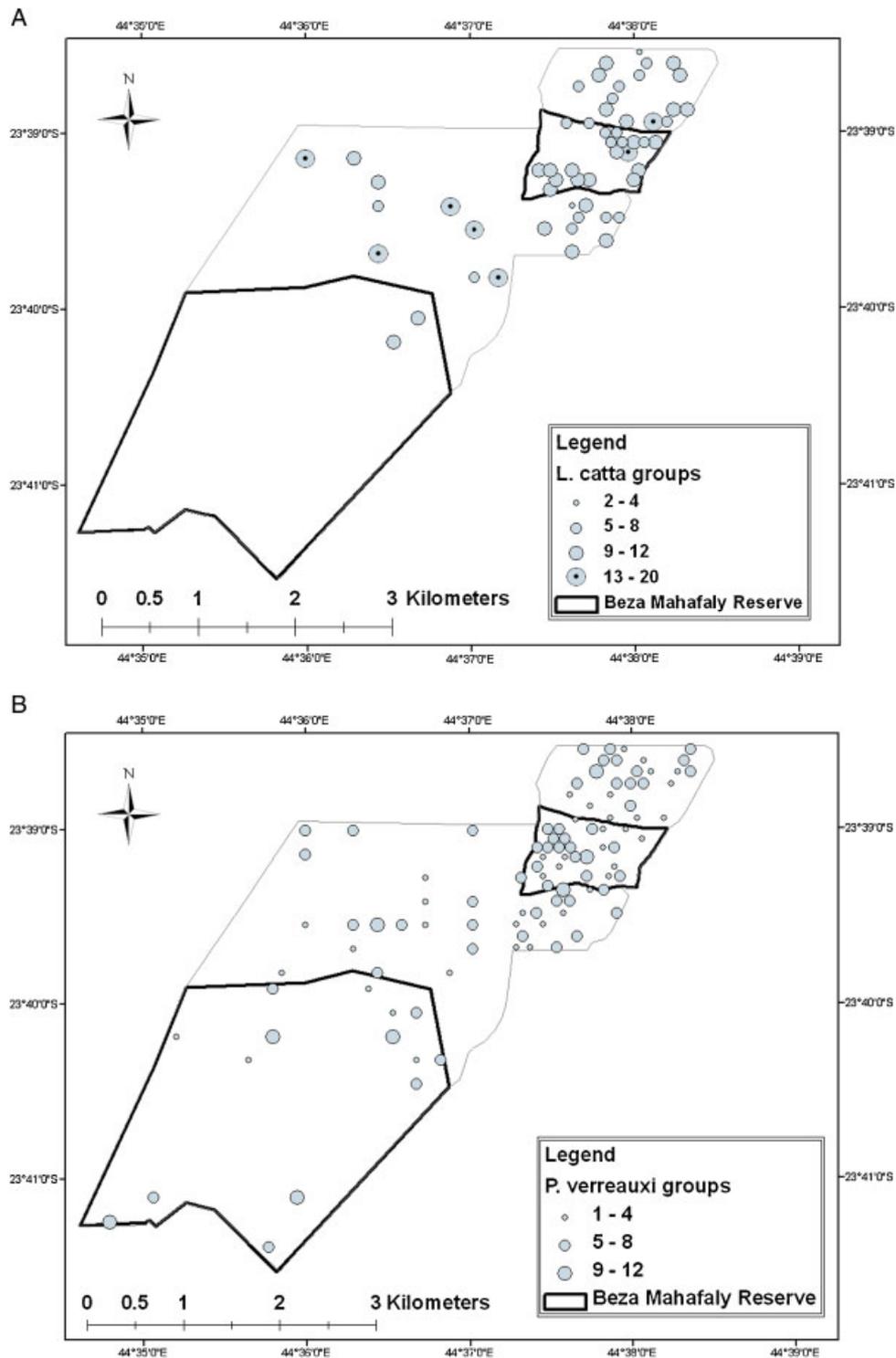


Fig. 2. (A) *L. catta* group size at sample points. Dot size is proportional to the number of individuals in the group. (B) *P. verreauxi* group size at sample points. Dot size is proportional to the number of individuals in the group.

detectability by time of day, year, or group size. *L. catta* and *P. verreauxi* densities were not significantly different from one another within the six regions located closest to the river (Regions 1–6); yet,

P. verreauxi density was significantly higher than that of *L. catta* in the drier western region (Regions 7 and 8) (Table II, Fig. 1). *L. catta* density was higher in regions located along the Sakamena River

TABLE II. Comparison of *L. catta* and *P. verreauxi* Density by Mixed-Forest Sampling Regions Illustrated in Figure 1. Paired-Tests for Differences in Density by Region were Performed Using a Z-Test Approximation of Sattthewaithe's Approximation

Comparison	<i>L. catta</i>		<i>P. verreauxi</i>		Z statistic	P
	Density (lemurs/ha)	Standard error	Density (lemurs/ha)	Standard error		
Regions 1–6	2.16	0.82	2.33	0.67	0.16	0.87
Regions 7 and 8	0.36	0.19	1.99	0.49	–3.08	<0.001
	Protected		Unprotected			
	Density (lemurs/ha)	Standard error	Density (lemurs/ha)	Standard error		
<i>L. catta</i>						
Region 2 vs. 1	3.57	1.01	2.75	0.81	0.63	0.53
<i>L. catta</i>						
Region 5 vs. 4	0.77	0.35	0.17	0.17	1.54	0.12
<i>P. verreauxi</i>						
Region 2 vs. 1	2.08	0.56	2.56	0.60	–0.59	0.55
<i>P. verreauxi</i>						
Region 5 vs. 4	3.26	0.97	0.68	0.49	2.36	0.02

(Regions 1–3) than in others (Table IIIA, Fig. 1), and *L. catta* were absent from Parcel II, the driest part of the study area. *L. catta* density was highest in the eastern region of Parcel I (Region 2), comprising mainly protected gallery forest, and *L. catta* density decreased with distance from the Sakamena River (Fig. 3). *P. verreauxi* density was fairly uniform across the study area except for (1) notable low density in Region 4, unprotected density in Region 4 which is unprotected dry deciduous forest adjacent to intact gallery forest, and (2) high density in the mostly dry deciduous western regions of Parcel I (Region 5) (Table IIIB; Fig. 3).

Only four total observations were made at point samples in Region 9 and all were *P. verreauxi*; therefore, these data were excluded from the analysis, because the detection function could not reliably be modeled in an area of that size (427 ha) using only four data points. However, *P. verreauxi* groups were detected between point sample transects in spiny forest, and reserve staff camped in Parcel II frequently observed *P. verreauxi* groups in nearby spiny forest at the southern edge of the parcel. Despite their low density, *P. verreauxi* are considered permanent residents in this spiny forest by reserve staff who frequent the forest. Although no *L. catta* were observed from point samples in Region 9, signs of *L. catta* presence there included feces, footprints, and a skull.

Lemur Plot Density Estimates Within Forest Types

Vuong tests indicated that a ZINB model was the best of the candidate models, and only those results are presented here. Across the study area, *L. catta* plot density was significantly higher in the gallery

forest than that in the dry deciduous forest (Table IV). Sifaka plot density was also significantly higher in the gallery forest than in the dry deciduous forest (Table IV).

L. catta attained much higher plot densities (1–34 lemurs/ha) than did *P. verreauxi* (1–17 lemurs/ha) (Fig. 4); when body weight of individuals is accounted for, *L. catta* plot biomass is estimated at 2.2–75.1 kg/ha while *P. verreauxi* is 2.8–47.6 kg/ha. *L. catta* plot densities were higher in the gallery forest than in the dry deciduous forest (Table IV), and they generally decreased westwards across the study area to their lowest in the southwestern dry deciduous forests (Fig. 4). Concentrations of *L. catta* detections, coupled with high plot densities accounted for high density in the gallery forest. *L. catta* density was highest in the northeast corner of Parcel I—the core area of protected gallery forest, but it was also high in gallery/dry deciduous forest transition areas near the reserve camp. Outside the gallery forests, *L. catta* were often detected in the vicinity of patches of gallery forest.

Although *P. verreauxi* plot density was higher in the gallery forest than in the dry deciduous forest across the study area, *P. verreauxi* plot density was highest in the protected dry deciduous forest owing to the large number of detections there (2.32 lemurs/ha). As was the case with *L. catta*, the majority of *P. verreauxi* detections were in the dry deciduous and gallery forests near the river (Fig. 4). *P. verreauxi* plot density was remarkably uniform across forest types (4–11 lemurs/ha at nearly 70% of all sample points where *P. verreauxi* were detected).

Given that the vast majority of studies conducted on these two species have been in the gallery and dry deciduous forests within 1 km of a river [Jolly & Pride, 1999; Richard et al., 2002; Sauther

TABLE III. Distance Analysis Results by Region for (A) *L. catta* and (B) *P. verreauxi*. The Number of Groups is After Truncation of Data to Improve Goodness-of-Fit for Detection Function Modeling in DISTANCE Software. Density, lemurs/ha. Region Numbers Refer to Regions Identified in Figure 1

Region	Area (ha)	Gallery (%)	Dry (%)	Spiny (%)	Samples (no.)	Total effort	Groups (no.)	Average group size (%CV)	Encounter rates (%CV)	Probability of detection	Density (lemurs/ha)				
											Estimate	CV (%)	95% CI		
(A)															
1	95	89	8	0	60	120	17	9.0 (10.0)	0.14 (24.2)	0.36	2.7	30	56	1.5	4.9
2	57	81	18	0	53	106	18	9.7 (7.6)	0.17 (23.6)	0.36	3.6	28	58	2.0	6.2
3	45	56	38	0	31	62	9	7.0 (16.0)	0.14 (33.3)	0.36	2.2	39	21	1.0	4.9
4	33	5	92	2	21	42	1	7.0 (0.0)	0.02 (100)	0.36	0.2	100	16	0.0	0.5
5	31	13	87	0	27	54	6	8.5 (8.5)	0.11 (40.8)	0.36	0.8	46	18	0.3	1.9
6	19	4	95	0	12	24	1	11.0 (0.0)	0.04 (100)	0.36	0.5	100	16	0.1	2.7
7	528	0	83	2	89	178	8	13.3 (9.1)	0.04 (35.3)	0.36	0.5 ^a	41	22	0.2	1.2
8	304	0	80	9	53	106	1	0.0	0.00						
9	427	0	14	81	58	116	0	0.0	0.00		0.0				
(B)															
1	95	89	8	0	60	120	30	4.8 (8.1)	0.25 (18.3)	0.34	2.6	23	78	1.6	4.0
2	57	81	18	0	53	106	8	4.8 (10.8)	0.18 (23.0)	0.34	2.1	27	52	1.2	3.5
3	45	56	38	0	31	62	12	5.9 (10.3)	0.19 (28.9)	0.34	2.7	32	36	1.4	5.2
4	33	5	92	2	21	42	2	6.0 (0.0)	0.05 (70.7)	0.34	0.7	71	82	0.2	2.4
5	31	13	87	0	27	54	15	5.5 (8.7)	0.28 (25.8)	0.34	3.3	30	37	1.8	5.9
6	19	4	95	0	12	24	6	3.6 (23.0)	0.25 (40.8)	0.34	2.2	48	7	0.7	6.4
7	528	0	83	2	89	178	21	5.8 (8.7)	0.11 (22.4)	0.19	2.0	29	46	1.1	3.5
8	304	0	80	9	53	106	13	5.5 (12.0)	0.12 (27.7)	0.19	2.0 ^a	34	42	1.0	3.9
9	427	0	14	81	58	116	4	8.0 (13.5)							

^aToo few observations to calculate given the size of the region. CV, coefficient of variation; CI, confidence interval; df, degrees of freedom.

et al., 1999; Sussman, 1991], we felt it important to compare density by forest type and protection status in forests within 1 km of the Sakamena River

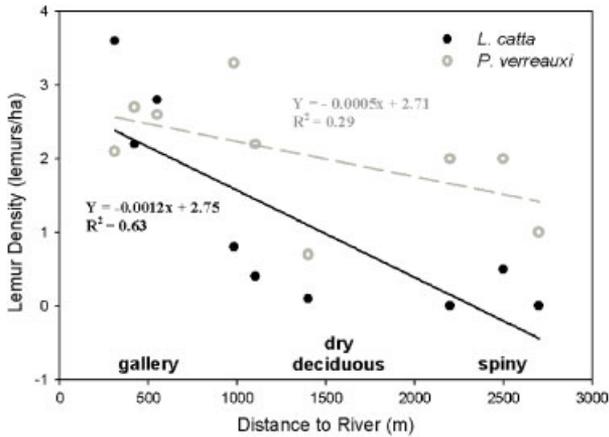


Fig. 3. Correlation between lemur density and distance to the river including corresponding forest type.

(Regions 1–6). There was a significant three-way interaction between forest type, species, and protection status, with *L. catta* in the protected gallery forest having the highest density, followed closely by *P. verreauxi* in the protected dry deciduous forests (Table II; Fig. 5). Within the protected area, *P. verreauxi* plot density was lower in the gallery than in the dry deciduous forest, whereas *L. catta* plot density was higher in the gallery and lower in the dry deciduous forest. This pattern was not observed in disturbed forests directly adjacent to Parcel 1, as the two species’ densities in these areas were not significantly different by forest type (Fig. 5).

In summary, both species were found in highest densities in Parcel I, and densities of both species were comparably lower in Parcel II than in other areas. *P. verreauxi* density was higher in dry deciduous forests than that of *L. catta*. *L. catta* density was not significantly higher than *P. verreauxi* in the gallery forest. Neither species attained high

TABLE IV. Comparison of Lemur Plot Density by Forest Type

Species	Dry forest		Gallery forest		Z statistic	P
	Plot density (lemurs/ha)	Standard error	Plot density (lemurs/ha)	Standard error		
<i>L. catta</i>	1.86	0.14	2.44	0.17	3.38	<0.001
<i>P. verreauxi</i>	1.59	0.09	1.88	0.13	2.19	0.03

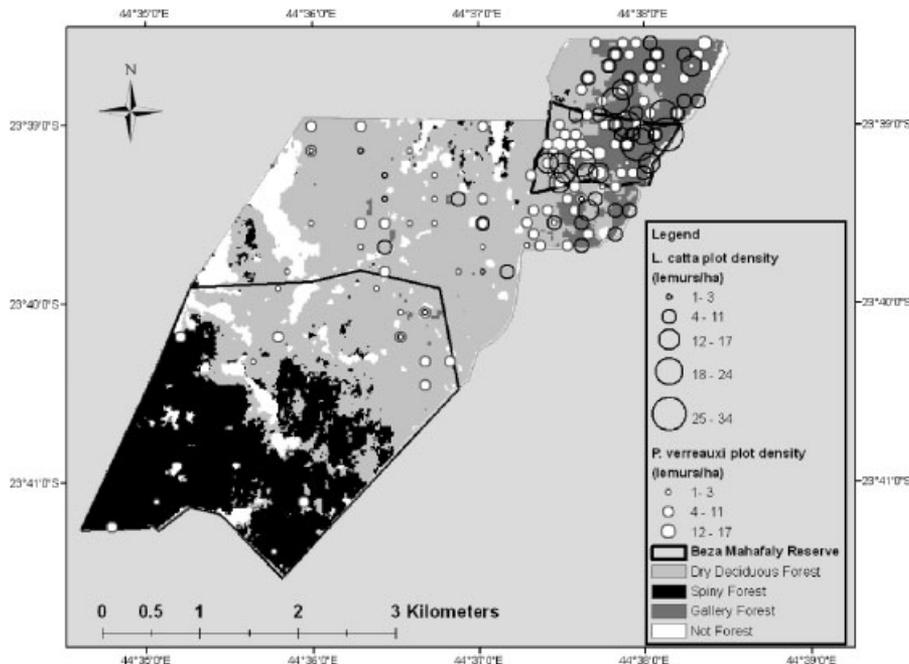


Fig. 4. *L. catta* and *P. verreauxi* plot density at each sample point, adjusted for probability of detection. Dot size is proportional to density.

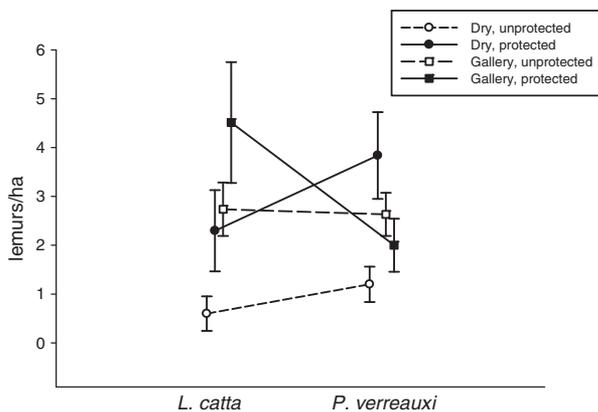


Fig. 5. Mean lemur plot density estimates by forest type in protected and unprotected in forest located within 1 km from the Sakamena River. Vertical segments extend over ± 1 standard error. (Significant three-way interaction between forest type, species, and protected area status ($Z = -0.909$, $P = 0.03$).)

density in the spiny forest, although *P. verreauxi* density was higher than that of *L. catta*.

DISCUSSION

Lemur Groups

Group size varies widely across primate species and even within some species. Although there are individual benefits to living in social groups (e.g., foraging advantages, predator avoidance, and cooperative defense against conspecifics), there are also significant disadvantages to group living, namely feeding competition [Chapman & Chapman, 2000].

Although there was no statistical difference in *L. catta* group size between gallery and dry deciduous forest types, evidence suggests there may be different determinants of group size at play within these two forest types.

At Berenty Reserve, Pride [2005] found that optimal *L. catta* group size was “intermediate” and that lemurs in small and large groups experienced greater levels of stress, as indicated by elevated cortisol levels. He also found that Berenty’s larger groups were found only in areas where intergroup conflicts over food resources were high. He speculated that members of large groups were stressed during the harsh season because their food resources were indefensible against other groups, but their group size was optimized over the long term.

At Beza Mahafaly Special Reserve, large groups (≥ 13) were found in both the gallery and dry deciduous forests. Large *L. catta* groups in the gallery forest were located in areas with both a high density of tamarind trees and conspecifics (2.7–3.6 lemurs/ha), whereas in the west, large groups were located in areas with low, if any, density of tamarind

trees and low density of conspecifics (~ 0.5 /ha). Large groups in the gallery forest seem to be “optimized” just as those at Berenty, described in Pride [2005]; that is, *L. catta* in large groups may benefit so greatly from their group size in high food abundance areas for the majority of the year that they are willing to incur high costs of group membership during the harsh dry season. In addition to foraging advantages, large group size in the gallery forest may also bestow greater protection to individuals against threats from conspecifics.

On the other hand, the only large *L. catta* groups observed in dry deciduous forests were located on the west side of the study area (Region 7), well away from the gallery forests along the river. Although the dry deciduous forests of Region 7 are spectrally similar to those of Regions 4–6, overall the forest canopy of Region 7 is much more open than that in Regions 4–6 [Axel, 2010]. In this region, intragroup competition for food resources is expected to be high, whereas intergroup competition for food is expected to be low. With low lemur density, food resources in this region may be easy to defend; however, travel time may be increased owing to large areas of nonforested land which may expose individuals to higher hawk predation pressure.

In addition, predation pressure by dogs is certainly higher in this region than at Berenty which is well-patrolled and frequented by many tourists [Pride, 2005]; and it is also likely to be higher than in Parcel I of BMSR. We encountered wild dogs in this region on multiple occasions (and once we were charged by a wild dog pack), but we encountered none in the east (although a dog attack on a juvenile *L. catta* was documented by another researcher in Parcel I during this study in 2006). Large group size in the dry deciduous forest may bestow foraging advantages, as well as greater protection against predators. In cases like this with easy food patch defensibility and/or high predation pressure, large groups may be favorable [Van Schaik, 1983].

P. verreauxi group size was higher in the dry deciduous forest than in the gallery, and groups were well-distributed throughout all but the driest portion of the study area. Richard and Heimbuck [1975] found that *P. verreauxi* territories often overlap and the spatial arrangement of *P. verreauxi* groups in this study, especially in the protected dry deciduous forest, supports their finding. Consequently, increased intergroup interactions would be expected in the deciduous dry forest. Larger group sizes may allow *P. verreauxi* to defend food patches, especially those that are only seasonally available. However, with information emerging about the incidence of infanticide in the species [Lewis et al., 2003; Littlefield, 2010], large group size may also provide greater protection for infants from males who regularly transfer between groups [Richard et al., 2002].

***Lemur catta* and *Propithecus verreauxi* More Segregated in Protected Habitat**

The two lemur species differed in distribution of plot densities across the study area; although *P. verreauxi* density was fairly uniform across forest types, *L. catta* plot density declined across the forest gradient from the river westwards to the spiny forest. This decline in *L. catta* plot density may be related to the decrease in the gallery forest moving west along the gradient. The distribution of *P. verreauxi* throughout the study area was relatively uniform across forest types, although plot density was highest at gallery-dry deciduous boundaries.

Outside the protected areas, there was quite a bit of overlap in species plot density, whereas there was much less species overlap in protected areas. This suggests there may be different mechanisms behind the coexistence of these two species, depending on forest protection status. Outside the protected areas, both species were often spotted feeding in close proximity to one another. Perhaps the open canopy allows for a greater diversity of tree species which accommodates the food preferences of both species, and thereby allows for greater food partitioning. Or perhaps, multiple groups foraging together may increase detection of predators. In protected areas, there seems to be some degree of spatial partitioning suggesting that multi-species group foraging may not be as beneficial there. It is not clear if differences in spatial patterns of distribution between protected and unprotected areas can be explained by food partitioning and corresponding habitat characteristics, so future work should address the mechanisms producing these patterns.

***Lemur catta* Density High in Gallery Forest Regardless of Status**

L. catta density was much higher in the gallery forest than in the dry deciduous forest, and this corresponds with earlier observations summarized in Sussman et al. [2006]. Yet, *L. catta* presence in the dry deciduous forest does not seem to be an anomaly, as they were detected at numerous locations in the dry deciduous forest at distances of up to 3 km from the Sakamena River.

L. catta density in the gallery forest of Parcel I was higher than that in the adjacent unprotected gallery forests (as well as other forest types); yet, *L. catta* density in the other two largely gallery forest regions (Regions 1 and 3) was still relatively high, suggesting that despite disturbance, the unprotected areas were functionally similar to the protected gallery forest. Unprotected gallery forest in this region is typically lost either to agriculture or to grazing activities. The loss forest to agriculture is swift and results in a sudden decline of the available gallery forest area, as trees are felled to make room

for crops. On the other hand, loss of the gallery forest to livestock grazing is a slow and insidious process, in which herders lop limbs off the gallery tree species for fodder. Canopy openness is greater in grazed gallery forests [Axel, 2010] which changes the forest microclimate, and tree seedlings are at a great risk of being trampled and/or eaten by livestock. In this way, the grazed gallery forest slowly shrinks in size over time. It is likely that densities of *L. catta* in unprotected habitats are the norm, because livestock grazing is an on-going activity in this region; contrastingly, *L. catta* density may be artificially high in those protected areas which exclude livestock grazing.

Some have speculated that *L. catta* predilection for *T. indica* [Gould, 2006], the dominant tree species in the gallery forest, is responsible for high *L. catta* density in that habitat, because there is often the expectation that population density is positively correlated with habitat preference [Cody, 1985; Fretwell, 1972]. There is, in fact, strong evidence to support the idea that the gallery forest is the preferred *L. catta* habitat [Gould, 2006], as even in regions characterized by mostly dry deciduous forest, many *L. catta* groups were located in close proximity to patches of the gallery forest, some of very small size (<1 ha).

Given that *L. catta* density declines with distance from the river, we should consider that their density may be correlated with some environmental gradient (e.g., soil moisture, foliar moisture), either directly or indirectly. *T. indica* density also declines with distance to the river [Sussman & Ratsirarson, 2006]. Merti-Milhollen et al. [2006] investigated tamarind resources in relation to proximity to water at Berenty Private Reserve, a forest very similar in composition to BMSR, and found that water and nitrogen content of mature tamarind leaves available during the *L. catta* birth season (dry season) were significantly correlated with proximity to the river, whereas fruit abundance was not. They also reported that *L. catta* foraging was correlated with tamarind leaf water and protein content, suggesting that *L. catta* may be selecting tamarind leaves of a certain condition.

Despite the fact that *T. indica*, a gallery species, represents an important element of the *L. catta* diet [Sauther, 1998; Yamashita, 2002], *L. catta* density still may not correlate with high-quality habitat. In fact, their density may not reflect habitat preference or be positively correlated with fitness [Pulliam, 1988; van Horne, 1983]. Without actual survival and fitness data, we cannot assume that the gallery forest is the highest quality habitat for *L. catta* at BMSR. However, there are some related survival data that may provide further insight into the issue.

Both Jolly et al. [2002] and Koyama et al. [2001] described differential survival of *L. catta* infants at Berenty Private Reserve. Mean 1-year infant

mortality was 32.5–37.0% in the gallery forest adjacent to tourist areas (with food and water provisions), whereas it was higher than 50% in the dry deciduous forest [Jolly, 2003a]. Gould et al. [2003] reported a similar mean infant mortality (52%) at BMSR. *L. catta* seem to benefit from food and water provisioning by people. We have observed individuals and groups raiding crops, scavenging trash, stealing food from kitchens, and drinking from myriad anthropogenic water sources, and documented their presence in high density along the southern edge of Parcel I near the camp.

Tourist and camp facilities are located close to the gallery forest at both BMSR and Berenty. Purposeful food provisioning by tourists at Berenty was common until the practice was banned in 1999 [Pinkus et al., 2006]; water provisioning for lemurs in forest troughs continued in 2007. *L. catta* at Berenty still manage to obtain food by stealing and trash-raiding. In recent years, *L. catta* at BMSR have also begun raiding trash cans and stealing unattended pieces of fruit; frequently, they can be seen drinking water out of pails in the camp. So, do higher quality food resources (i.e., gallery forest) bestow higher fitness on gallery groups such that they have a competitive advantage at securing anthropogenic resources? Or do gallery groups simply benefit by their spatial proximity to anthropogenic resources? The question remains whether high *L. catta* density in the gallery forest is owing to proximity to human-provided resources (unintended food and water provisioning) or owing to reasons unrelated to human presence.

CONCLUSION

Lemur density estimates from protected gallery forests from this study are in line with other published estimates [Gould, 2006; Jolly et al., 1982; Jolly & Pride, 1999; Sussman, 1991]; however, results from sampling multiple forest types of different protection status suggest that there is disparity between lemur density in protected areas and disturbed forests, as well as across forest types.

If one were to generalize density results obtained from protected forests to unprotected forests, both *P. verreauxi* and *L. catta* density would be overestimated. The good news is that our data show that both species occupy unprotected areas, sometimes at even higher densities than protected areas; but in the absence of data on survivorship and fecundity, we cannot eliminate the possibility that unprotected areas are acting as ecological sinks—very low-quality habitat unable to support a population on its own that persists owing to individuals immigrating from high-quality habitat [Pulliam, 1988].

Results from this study indicate that information collected on populations in the protected gallery forest may not be representative of populations living either in unprotected gallery forest or in dry

deciduous forest. There is no doubt that long-term studies on protected populations have provided us with invaluable information on both species' ecology and behavior, but it is important that some researchers move beyond the protected populations and collect information on groups living in forests more representative of the two populations as a whole. Without this information, we cannot fully understand species requirements for the large majority of the remaining populations of these two species, and we cannot hope to design effective conservation plans.

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