

The lemurs of the Ambatovy-Analamay region

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Abstract

Rapid biological assessments were conducted to evaluate lemur species occurring in nine different habitats in the Ambatovy-Analamay forest. The main goal of this study was to assess lemur diversity in order to compare these data with the forthcoming results for the Ankerana forest (a proposed conservation zone). The various lemur species found in the Ambatovy-Analamay forest have broad distributions across the central eastern humid forests and the Central Highlands. Twelve lemur species were observed, including four diurnal (*Indri indri*, *Propithecus diadema*, *Varecia variegata*, and *Hapalemur griseus*), two cathemeral species (*Eulemur fulvus* and *E. rubriventer*) and six nocturnal species (*Avahi laniger*, *Lepilemur mustelinus*, *Cheirogaleus major*, *Microcebus lehilahytsara*, *Allocebus trichotis*, and *Daubentonia madagascariensis*). The presence of *Daubentonia madagascariensis* was inferred based on feeding signs and sleeping nests. The maximum number of species in any habitat was 10, including the Azonal Impacted Good Quality, Transitional Benchmark, Transitional Impacted Good Quality, and Zonal Benchmark. No primate species was found in the Azonal Impacted Degraded habitat, which consists largely of *Erica* scrub. In general, the number of lemur species and their densities vary with the level of habitat degradation.

Keywords: Lemurs, species diversity, biogeographic affinities, Ambatovy-Analamay forest, Madagascar

Résumé

Une évaluation rapide de la population de lémuriens dans neuf différents types d'habitat du site minier d'Ambatovy-Analamay a été menée par l'association Vahatra. Le but de cette étude fut de répertorier la diversité de lémuriens dans cette zone afin de la comparer avec les résultats prochainement

obtenus dans la forêt d'Ankerana (future zone de conservation). La méthode de capture-relâche des espèces nocturnes (*Microcebus*, *Cheirogaleus*, *Allocebus*) a été également adoptée afin d'identifier les espèces nocturnes sympatriques. Le coefficient de Jaccard est la méthode statistique utilisée pour savoir s'il y a un rapport entre la richesse spécifique et le type d'habitat.

Douze espèces de lémuriens, largement distribuées dans les forêts humides du Centre-est et des hauts plateaux malgaches, ont été enregistrées dans la forêt d'Ambatovy-Analamay, dont quatre espèces diurnes (*Indri indri*, *Propithecus diadema*, *Varecia variegata*, *Hapalemur griseus*), deux espèces cathémérales (*Eulemur fulvus*, *E. rubriventer*) et six espèces nocturnes (*Avahi laniger*, *Lepilemur mustelinus*, *Cheirogaleus major*, *Microcebus lehilahytsara*, *Allocebus trichotis* et *Daubentonia madagascariensis*). La présence de *Daubentonia madagascariensis* a été basée sur des traces d'alimentation et des vieux nids. Les autres espèces connues sur le versant oriental malgache, entre autres *Lepilemur microdon*, *Prolemur simus* et *Cheirogaleus crossleyi* n'étaient pas observées. Seul *Microcebus lehilahytsara* était l'espèce nocturne capturée durant l'étude. Le nombre maximum d'espèces (10) a été observé dans l'habitat « Azonal Impacted Good Quality », « Transitional Benchmark », « Transitional Impacted Good Quality » et « Zonal Benchmark ». Toutefois, aucune espèce de lémurien n'a été trouvée dans l'habitat « Azonal Impacted Degraded », qui est constituée en grande partie par une formation monoculture d'*Erica*. La richesse spécifique élevée dans certains types d'habitat pourrait être expliquée entre autre par la présence des grands arbres qui constituent à la fois une source de nourriture et des supports pour les lémuriens de grande forme. Bien que d'autres aspects écologiques entrent en grande partie dans l'explication de la densité, la diminution de la densité dans un milieu, plus particulièrement celle des lémuriens diurnes, est certainement due, entre autres aux pressions humaines (exploitation des grands arbres et pâturage).

Mots clés : Lémuriens, diversité spécifique, affinité biogéographique, forêt d'Ambatovy-Analamay, Madagascar

Introduction

The advancement of effective conservation programs for the unique habitats of Madagascar should be based on solid information concerning the distribution and abundance of the island's biota. The Ambatovy-Analamay forest is localized at the edge of the Ankeniheny-Zahamena forest corridor, which has been the subject of considerable recent research and conservation action. Due to particular aspects of its ultrabasic soils, the Ambatovy-Analamay region contains distinct vegetation in comparison to other central eastern humid forests at the same elevation and the question remains as to what influence this might have on the structure and composition of the local vertebrate communities. One aspect of this current project is to answer this question in relation to the local primate species.

The Ambatovy area is the subject of a large-scale mining project associated with exploitation of nickel and cobalt deposits. Lemurs have been one of the focal taxa groups associated with the environmental impact studies organized by this project (see Mass *et al.*, p. 192). Even though for several decades lemurs have been the focus of biological research in the Andasibe area, one primate species new to science, *Microcebus lehilahytsara*, has been recently discovered in the area (Kappeler *et al.*, 2005).

Associated with the mineral exploitation project in the Ambatovy-Analamay forest, a biodiversity conservation project has been proposed in the Ankerana forest associated with the Ambatovy project's offset program (see Dickinson & Berner, p. 2). Hence, another aspect of the current project was to obtain baseline information on the species richness and density of lemurs in the Ambatovy-Analamay forest, which will be compared to data obtained in forthcoming inventories in the Ankerana area. Herein, particular attention is given to patterns of density and diversity in a variety of different habitat types within the Ambatovy-Analamay forest, paying particular attention to levels of anthropogenic pressure that might have direct and indirect impacts on local primate species richness.

Methods

Dates

The series of primate surveys reported herein were undertaken between 6 January and 21 February 2009 in the Ambatovy-Analamay region.

Forest habitats

The forest type classification used herein is that of the Ambatovy project, which is discussed in Goodman & Raselimanana (pp. 36-37).

Line transects

For each habitat type in the Ambatovy-Analamay study zone, 1-3 transects of different lengths were installed (Table 1). Lines were marked with flags every 100 m, in order to determine the distance of any given observation along the transect. The geographical coordinates of each transect were recorded at 100 m intervals.

The line transect method is effective for locating different nocturnal and diurnal species by observation or vocal identification. Transect work was conducted during the day between 06h00 and 10h00 and again between 15h00 and 18h00, while nocturnal work was carried out between 19h00 and 22h00. For each lemur encountered (visual or acoustic), the following variables were recorded: time of contact, species, number of individuals, their estimated height above the ground, behavior, the distance of the animal(s) from the transect line, and the age and sex composition of the group (when possible). Further, feeding signs or nests of certain lemurs are rather diagnostic, such as *Daubentonia madagascariensis*, and information on their distribution and location were noted.

Capture-release

The capture-release method was used for small nocturnal lemurs of the genera *Microcebus*, *Cheirogaleus*, and *Allocebus*. The capture-release technique can provide detailed data on habitat preferences of the different taxa and the means to determine whether congeneric species occur in sympatry.

Two different live trap types were employed: Sherman traps with the dimensions of 22.5 cm x 8.6 cm x 7.4 cm and National (Tomahawk) traps measuring 39.2 cm x 12.3 cm x 12.3 cm. The traps were installed along the transect lines for 6-8 consecutive nights, with a ratio of 3-4 Sherman traps to 1 National trap. Each trap was installed at a fixed position along the transect line, with an associated flag bearing a unique number. The traps were placed 1-2 m off the ground, on tree trunks, branches, and lianas and were baited with segments of fresh banana. In all cases, they were installed in forest habitats with the exception being the Azonal Benchmark habitat, which consisted of degraded forest.

Table 1. Number of transect walks at night and during the day in the Ambatovy-Analamay region. ABE = Azonal Benchmark, AIG = Azonal Impacted Good Quality, AID = Azonal Impacted Degraded, TBE = Transitional Benchmark, TIG = Transitional Impacted Good Quality, TID = Transitional Impacted Degraded, ZBE = Zonal Benchmark, ZIG = Zonal Impacted Good Quality, and ZID = Zonal Impacted Degraded.

Habitat	Transect ID	Length (m)	Diurnal	Nocturnal
ABE	T 5	500	1	2
	T 6	1000	8	2
	T 7	1000	8	2
AIG	T15	1000	6	3
AID	T 2	1000	0	2
TBE	T 3	1000	5	5
	T 4	700	6	4
TIG	T 1	1000	9	4
TID	T14	1000	6	2
ZBE	T 9	1000	7	2
	T10	1000	7	2
	T11	500	1	1
ZIG	T13	1000	4	2
ZID	T 8	1000	7	2
	T12	500	1	1

Traps were visited daily just after dawn. Trapped animals were brought back to the field camp, measured, weighed, feed during the day, and then released at the exact capture location. Traps were re-baited daily in the later portion of the afternoon. A lemur “trap-night” is defined as one trap in service from dusk to dawn, a period of approximately 12 hours. All captured animals were photographed and the following morphological measurements were made: ear length, hindfoot length (without claws), and tail length (end of tail bone). Tissue samples (small pieces of the ear and fur) were collected from each captured individual. The species identification of each animal was confirmed based on molecular genetic studies in the laboratories of Dr. Peter Kappeler (Göttingen, Germany) and Dr. Anne Yoder (Durham, North Carolina, USA).

Density calculation

The method used to calculate the density of each species observed along a transect is based on Whitesides *et al.* (1988):

$$D = n / 2WL$$

where n = number of individuals of a species, W = mean perpendicular distance of all of the individuals of the species at the transect, and L = length of the transect

Individuals/species noted based only on vocalizations are not included in the density calculation, as it is possible that they could

be counted more than once during the same transect pass, inflating results (Burnham *et al.*, 1980; Whiteside *et al.*, 1988; Buckland *et al.*, 1993). To reduce the influence of certain climatic factors on density calculations, data obtain during the day transects during periods of rain were not included in the analyses.

Taxonomy and vernacular names

In general, we followed the systematic arrangement at the generic and species level published in Mittermeier *et al.* (2006). Local assistants and members of the Ambatovy project field staff provided the local vernacular names.

The state of each habitat type and anthropogenic pressures

For each transect, a temporary plot (10 x 10 m) was placed every 100 m to measure vegetational parameters including the number of trees, visual estimation of diameter at breast height (dbh) based on three size ranges (between 5 and 10 cm, between 10 and 20 cm, and greater than 20 cm), the surface area covered by trees, the structure of the understory (0: open, 1: dense), and the presence of lianas and bamboo (0: absent, 1: rare, 2: abundant, 3: very abundant). Additionally, the number of cut trees (either toppled or with remaining trunk) and cattle signs (direct observations, tracks, dung) were also noted.

Data analysis

In order to understand the faunistic relationships between the lemur taxa occurring within the different habitat types, the Jaccard Index was used to analyze the field data, based on the following formula:

$$I = C / (N_1 + N_2 - C)$$

where N_1 = specific richness in habitat type 1, N_2 = specific richness in habitat type 2, and C = number of species occurring in both habitats.

The associated coefficients, based on presence-absence data, were entered into the Cluster Analysis program (method = Euclidean distance; complete linkage) of SYSTAT 10.0 to produce a branching diagram illustrating the faunistic similarities of lemurs in the different vegetation types, and between different forest blocks across the central eastern humid forests and the Central Highlands of Madagascar.

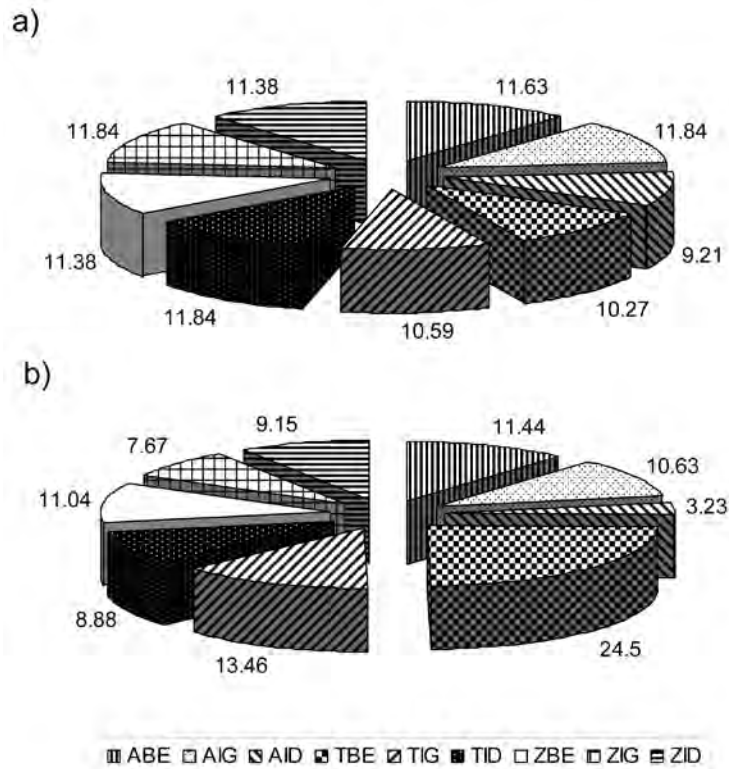


Figure 1. Pie diagrams based on percentage of surveyed distances in the different habitat types for **a)** diurnal transects and **b)** nocturnal transects. ABE = Azonal Benchmark, AIG = Azonal Impacted Good Quality, AID = Azonal Impacted Degraded, TBE = Transitional Benchmark, TIG = Transitional Impacted Good Quality, TID = Transitional Impacted Degraded, ZBE = Zonal Benchmark, ZIG = Zonal Impacted Good Quality, and ZID = Zonal Impacted Degraded.

Table 2. Presence-absence data for the different lemur species in the Ambatovy-Analamay region during the January-February 2009 inventories based on habitat types. + = species present, - = species absent, * = feeding signs, § = species only heard, £ = species only observed by other members of the inventory team. ABE = Azonal Benchmark, AIG = Azonal Impacted Good Quality, AID = Azonal Impacted Degraded, TBE = Transitional Benchmark, TIG = Transitional Impacted Good Quality, TID = Transitional Impacted Degraded, ZBE = Zonal Benchmark, ZIG = Zonal Impacted Good Quality, and ZID = Zonal Impacted Degraded.

Family	Species	Vernacular name	ABE	AIG	AID	TBE	TIG	TID	ZBE	ZIG	ZID	IUCN (2007)
Cheirogaleidae	<i>Microcebus lehilahytsara</i>	antsidy	+	+	-	+	+	+	+	+	+	DD
	<i>Allocebus trichotis</i>	antsidy	-	+	-	+	-	-	-	-	-	DD
	<i>Cheirogaleus major</i>	tsitsihy	+	+	-	+	+	+	+	+	+	DD
Lepilemuridae	<i>Lepilemur mustelinus</i>	hataka	+	+	-	+	+	+	+	+	+	DD
Lemuridae	<i>Hapalemur griseus</i>	kotrika	+	+	-	+	+	+	+	+	+	LC
	<i>Eulemur fulvus</i>	varikamavo	+	+	-	+	+	§	+	+	+	NT
	<i>E. rubriventer</i>	varikamena	+	§	-	+	+	+	+	-	-	VU
	<i>Varecia variegata</i>	varikanda	-	-	-	-	-	-	+	-	+	CR
Indriidae	<i>Propithecus diadema</i>	simpona	+	+	-	+	+	+	+	-	£	EN
	<i>Avahi laniger</i>	matoriandro	+	+	-	+	+	-	+	+	+	LC
	<i>Indri indri</i>	babakoto	+	+	-	+	+	-	+	§	£	EN
Daubentoniidae	<i>Daubentonia madagascariensis</i>	aye aye	*	-	-	-	*	-	-	-	-	NT
	TOTAL		10	10	0	10	10	7	10	7	9	

CR: Critically Endangered, EN: Endangered, NT: Near Threatened, VU: Vulnerable, LC: Least Concern, and DD: Data Deficient

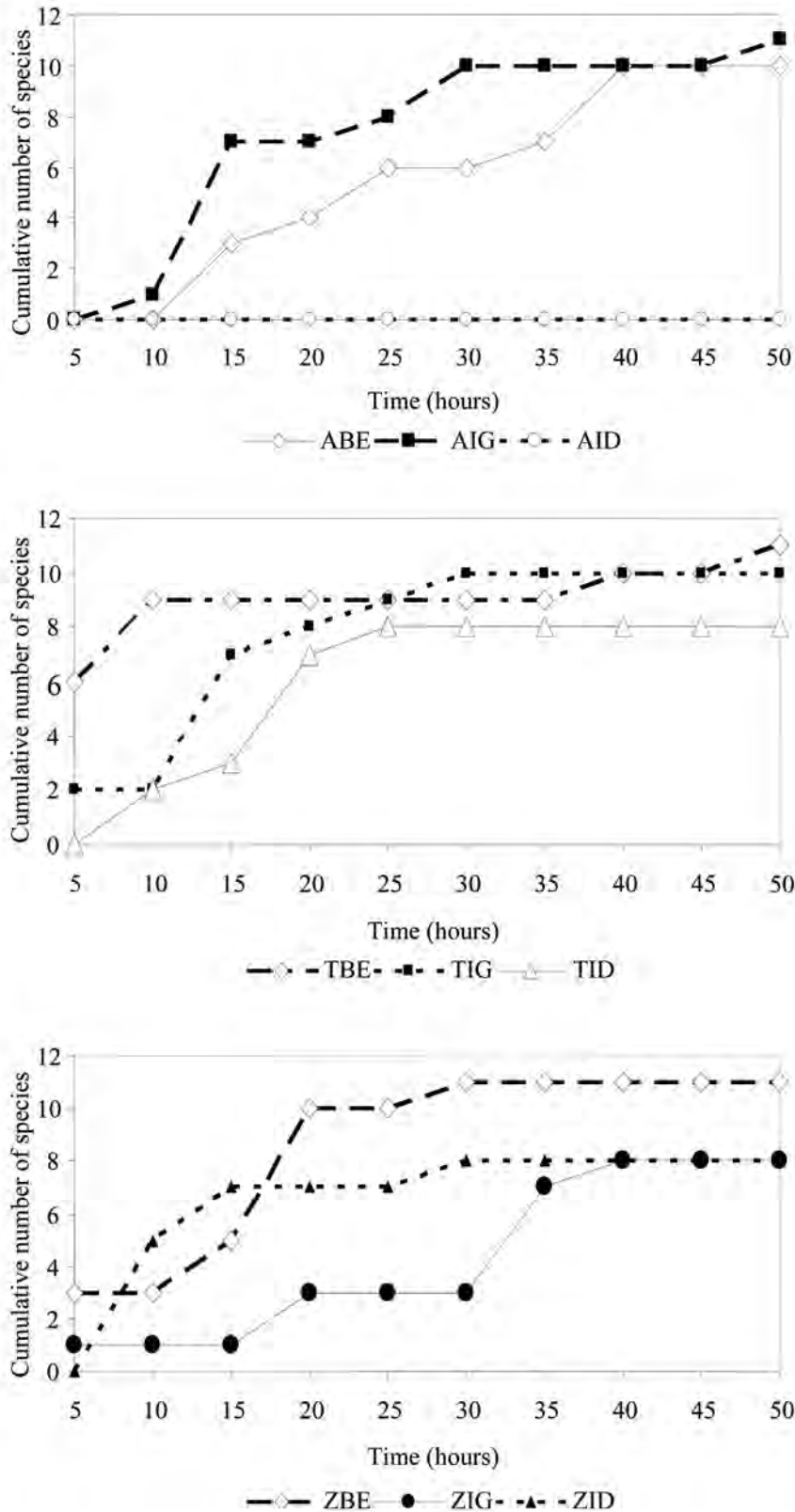


Figure 2. Lemur species accumulation curves for the nine different vegetation formations within the Ambatovy-Analamay region. ABE = Azonal Benchmark, AIG = Azonal Impacted Good Quality, TBE = Transitional Benchmark, TIG = Transitional Impacted Good Quality, TID = Transitional Impacted Degraded, ZBE = Zonal Benchmark, ZIG = Zonal Impacted Good Quality, and ZID = Zonal Impacted Degraded.

Results

A total of 442 hours of transect observations were made during this study. Further, 72.7 km of transect line were censused during the day (Figure 1a) and 32.8 km of transect line during the night (Figure 1b).

Lemur observations

Species richness

Twelve species of lemur, distributed in five different families, were found in the Ambatovy-Analamay forest (Table 2). These include four diurnal taxa (*Indri indri*, *Propithecus diadema*, *Varecia variegata*, and *Hapalemur griseus*), two cathemeral species (*Eulemur fulvus* and *E. rubriventer*), and six nocturnal species (*Avahi laniger*, *Lepilemur mustelinus*, *Cheirogaleus major*, *Microcebus lehilahytsara*, *Allocebus trichotis*, and *Daubentonia madagascariensis*). The latter species was not directly observed, but its presence was inferred based on feeding signs and old sleeping nests.

The maximum number of species observed in a single vegetation type was 10, which occurred in the Azonal Impacted Good Quality, Transitional Benchmark, Transitional Impacted Good Quality, and Zonal Benchmark habitats. No lemur species was found in the Azonal Impacted Degraded vegetation type. Other lemur species have been reported in the Ambatovy-Analamay forest (Rapport Ambatovy, 2007), which include *Lepilemur microdon*, *Prolemur simus*, and *Cheirogaleus crossleyi*, but these were not recorded during our study.

Species accumulation curves

The species accumulation curves for the different lemur taxa in the various habitat types are presented in Figure 2. These types of curves provide insight into the completeness of a given inventory with regards to the number of additional species recorded from a site or habitat as a function of effort. The following aspects can be interpreted from these curves:

- 1) For the azonal habitats (n=3), an additional species was added to the local fauna of the Azonal Impacted Good Quality after 45 hours of observation, while no further species was added to the Azonal Benchmark after 35 hours.
- 2) For the transitional habitats (n=3), measures of species richness in each habitat generally accrued rapidly with no new species in the Transitional Impacted Degraded after 25 hours of effort and in the Transitional Impacted Good Quality after 30 hours of effort. In the case

of the Transitional Benchmark habitat, nine species were recorded after 10 hours of effort, one additional species was added after 35 hours, and a final species after 45 hours.

- 3) For the zonal habitats (n=3), species accumulation curves increased slowly, with plateaus for the Zonal Benchmark and Zonal Impacted Degraded reached after 30 hours and for the Zonal Impacted Good Quality after 40 hours.

Frequency of observation of different lemur species

Over the 325 observations conducted during the study, no lemur species was recorded in the Azonal Impacted Degraded habitat. Lemur species were occasionally observed in the Transitional Impacted Degraded, Zonal Impacted Degraded, and Zonal Impacted Good Quality habitats. However, the majority of observations of lemurs were made in the Transitional Benchmark, Transitional Impacted Good Quality, and Zonal Benchmark habitats.

For the nocturnal species, *Microcebus lehilahytsara* was commonly observed in the Azonal Impacted Good Quality and Transitional Benchmark habitats, as well as several other habitats, while *Allocebus trichotis* was only recorded in these two habitats and was notably rarer. For the diurnal species, certain species were broadly distributed, such as *Hapalemur griseus*, which was found in all eight forested habitats. On the opposite extreme, certain species only occurred in a limited number of habitats, such as *Varecia variegata*, which was only recorded in two of the eight forested habitats.

Certain natural history characteristics of diurnal lemur species

Indri indri – Group size varied between two and five individuals [2.1 ± 1.1 individuals, n (number of groups) = 14]. This species was most frequently observed in the Transitional Impacted Good Quality habitat. Single babies, dependent and carried on their mothers' backs, were observed in the groups found in the Transitional Impacted Good Quality, Azonal Benchmark, and Azonal Impacted Good Quality habitats.

Propithecus diadema – Group size varied between two and six individuals [3.7 ± 1.3 individuals, n = 24]. Groups were observed in the Azonal Benchmark, Azonal Impacted Good Quality, Transitional Benchmark, Transitional Impacted Good Quality, and Zonal Benchmark habitats. During the period of our

inventories, young attached to their mothers' back were observed on numerous occasions.

Varecia variegata – Groups of this species were only observed in the Zonal Impacted Degraded and Zonal Benchmark habitats. In virtually all cases, they could not be approached within 20 m. However, their local presence was easily documented based on the roaring vocalizations of males.

Eulemur fulvus – Group size varied between four and 15 individuals [6.9 ± 3.8 individuals, n (number of groups) = 14]. No clear external pattern of sexual dimorphism in adults was noted. Groups were composed of adult and subadult males and females and numerous dependent offspring. Observations were most common in the Azonal Benchmark, Transitional Benchmark, and Zonal Benchmark habitats. The presence of this species in the Transitional Impacted Degraded habitat was based on one vocalization.

Eulemur rubriventer – This species was most frequently observed in the Transitional Impacted Good Quality and Azonal Benchmark habitats. Group size varied between two and five individuals [3.4 ± 1.3 individuals, $n = 11$].

Hapalemur griseus – Groups of up to six individuals were observed [3.4 ± 1.9 individuals, $n = 43$], generally composed of one adult male, adult females, and their young. This species, observed in all of the eight forested habitats, was more frequently noted in valleys, where new growth bamboo was common.

Capture results

The results from live trapping of small nocturnal lemurs are presented in Table 3. In total, nine

individual lemurs were captured during 1670 lemur trap-nights, resulting in a trap capture success rate of 0.5%. Trapping success varied between transect lines from 0.3 to 1.3%. *Microcebus lehilahytsara* was the only primate species trapped. In all cases, trap placements that resulted in the capture of *Microcebus* were in open areas of the forest, with respect to the canopy and understory vegetation. In addition, four species of endemic small mammals, including three rodents of the family Nesomyidae (*Eliurus grandidieri*, *E. tanala*, and *E. webbi*), a shrew-tenrec of the family Tenrecidae (*Microgale talazaci*), and a species of introduced rodent of the Family Muridae (*Rattus rattus*) were caught (see Soarimalala & Raheeriarisena, p. 153).

Density estimates

A summary of the density calculation for the different lemur species based on habitat is presented in Table 4. These data show that there is considerable variation within and between species in density measures. The highest densities of *Microcebus lehilahytsara* were found in the Zonal Impacted Degraded and Azonal Impacted Good Quality habitats, for *Allocebus trichotis* in the Transitional Benchmark habitat, *Cheirogaleus major* and *Lepilemur mustelinus* in the Zonal Impacted Good Quality habitat, *Avahi laniger* in the Transitional Impacted Good Quality habitat, *Hapalemur griseus* in the Azonal Impacted Degraded and Transitional Impacted Degraded habitats, *Eulemur rubriventer* in the Transitional Impacted Good Quality habitat, *E. fulvus* in the Azonal Impacted Good Quality habitat, *Propithecus diadema* in the Azonal Benchmark

Table 3. Summary of small nocturnal lemur trapping success. Trap lines were set in seven of the different habitat types represented in the Ambatovy-Analamay forest.

Habitat	Number of nights	Number of traps used	Number of trap-nights	Number of lemurs captured	Lemurs species	Capture rate of lemurs (%)	Number of other mammals captured
Azonal Impacted Good Quality	6	25	150	0	None	0	3 ^{1,2,3}
Azonal Benchmark	7	50	350	2	<i>M. lehilahytsara</i>	0.6	1 ²
Transitional Benchmark	8	50	400	1	<i>M. lehilahytsara</i>	0.3	1 ³
Transitional Impacted Good Quality	8	40	320	2	<i>M. lehilahytsara</i>	0.6	1 ³
Zonal Benchmark	6	25	150	2	<i>M. lehilahytsara</i>	1.3	0
Zonal Impacted Good Quality	6	25	150	0	None	0	4 ^{3,4,5}
Zonal Impacted Degraded	6	25	150	2	<i>M. lehilahytsara</i>	1.3	0
	47		1670	9		0.5	

¹ *Microgale talazaci*

⁴ *Eliurus webbi*

² *Rattus rattus*

⁵ *Eliurus grandidieri*

³ *Eliurus tanala*

Table 4. Estimated mean densities (individuals/km²) of the different lemur species observed during the transect line in the Ambatovy-Analamay forest. Records based on vocalizations are not included. ABE = Azonal Benchmark, AIG = Azonal Impacted Good Quality, TBE = Transitional Benchmark, TIG = Transitional Impacted Good Quality, TID = Transitional Impacted Degraded, ZBE = Zonal Benchmark, ZIG = Zonal Impacted Good Quality, and ZID = Zonal Impacted Degraded.

Species	ABE	AIG	TBE	TIG	TID	ZBE	ZIG	ZID
<i>Microcebus lehilahytsara</i>	483	620	291	451	141	462	301	719
<i>Allocebus trichotis</i>	0	23	89	0	0	0	0	0
<i>Cheirogaleus major</i>	81	141	103	180	83	117	392	129
<i>Lepilemur mustelinus</i>	70	85	131	51	63	44	138	133
<i>Avahi laniger</i>	10	95	67	235	0	101	172	140
<i>Haplemur griseus</i>	42	270	165	76	211	88	143	94
<i>Eulemur rubriventer</i>	31	0	16	130	17	48	0	0
<i>E. fulvus</i>	79	119	52	61	0	84	50	80
<i>Varecia variegata</i>	0	0	0	0	0	2	0	10
<i>Propithecus diadema</i>	133	63	25	132	92	68	0	0
<i>Indri indri</i>	17	11	0	44	0	20	0	0

Table 5. Data matrix of Jaccard Index coefficients for the lemur species in the eight different habitats of the Ambatovy-Analamay forest. Two habitat types have similar species if Jaccard Index coefficient is close to 1.000. ABE = Azonal Benchmark, AIG = Azonal Impacted Good Quality, TBE = Transitional Benchmark, TIG = Transitional Impacted Good Quality, TID = Transitional Impacted Degraded, ZBE = Zonal Benchmark, ZIG = Zonal Impacted Good Quality, and ZID = Zonal Impacted Degraded.

	ABE	AIG	TBE	TIG	TID	ZBE	ZIG
AIG	0.909						
TBE	0.909	1.000					
TIG	0.909	0.833	0.833				
TID	0.800	0.727	0.727	0.727			
ZBE	0.909	0.833	0.833	0.833	0.727		
ZIG	0.800	0.727	0.727	0.727	0.600	0.727	
ZID	0.818	0.750	0.750	0.750	0.636	0.909	0.800

habitat, and *Indri indri* in the Transitional Impacted Good Quality habitat.

Analysis of differences in lemur community composition between habitat types

The data matrix of Jaccard Index coefficients for the lemur species faunistic relationships in the eight different habitats is presented in Table 5. The intent of this analysis is to examine if the species composition of the lemur communities in the different habitats are similar or not. Figure 3 presents the resulting branching diagram associated with these coefficient data.

An examination of the dendrogram indicates that two distinctive groups were identified. The first group is formed by the three zonal habitats and the second group by two azonal habitats and three transitional habitats. In the second group, the Azonal Impacted Good Quality and Transitional Benchmark habitats

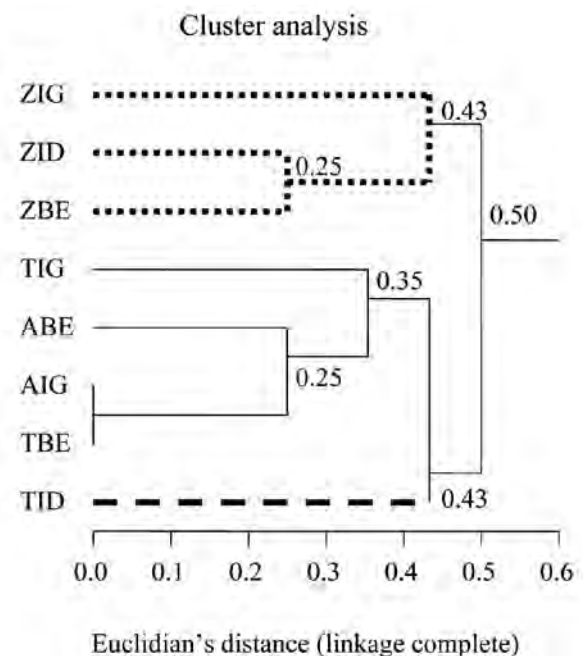


Figure 3. Branching diagram based on the Jaccard Index coefficients of the faunistic relationships of lemur communities within the different vegetation types of the study area in the Ambatovy-Analamay forest. ABE = Azonal Benchmark, AIG = Azonal Impacted Good Quality, TBE = Transitional Benchmark, TIG = Transitional Impacted Good Quality, TID = Transitional Impacted Degraded, ZBE = Zonal Benchmark, ZIG = Zonal Impacted Good Quality, and ZID = Zonal Impacted Degraded.

have identical lemur faunas, and the Transitional Impacted Degraded habitat is the outlier.

The state of each habitat type and anthropogenic pressures

In Figure 4, we present data for the nine different habitats in which the 100 m² plots were installed for the different height and diameter at breast height

(dbh) classes. The intent of these plots was to assess the level of anthropogenic impact.

- 1) The zonal formations have more trees than the azonal and transitional habitats,
- 2) In all habitats, the small dbh trees are more common than the other two size classes,
- 3) Tall trees (with a height of more than 10 m) are more numerous in the Azonal Impacted Good Quality, Transitional Impacted Degraded, Zonal Benchmark, Zonal Impacted Good Quality, and Zonal Impacted Degraded habitats; with values ranging between 14 - 18%,
- 4) The Azonal Impacted Degraded habitat does not contain any trees. This zone is dominated by *Erica* bushes,

- 5) For the three azonal habitats, the understory is dense and the surface area covered by trees is moderate ($\leq 50\%$). Further, lianas are generally absent and bamboos are variable. The number of cut trees is less than 2.7 per ha,
- 6) For the three transitional habitats, the surface area covered by trees is notably high ($\leq 70\%$) and the understory is generally open. Lianas and bamboo are rare. The number of cut trees is considerable, with a range of 2.1 - 8.1 per ha,
- 7) For the three zonal habitats, the surface area covered by trees is moderate (50%) and the understory is open in most cases. In general, lianas are abundant and bamboos are present. The number of cut trees is high, falling within the range of 4.8 to 13.6 per ha.

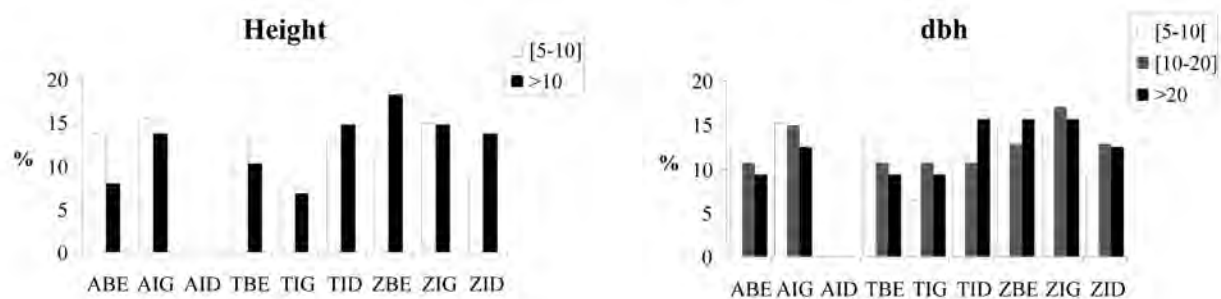


Figure 4. Distribution of two different tree parameters in the nine different habitat types in the Ambatovy-Analamay forest: height (left) and diameter at breast height [dbh] (right). ABE = Azonal Benchmark, AIG = Azonal Impacted Good Quality, AID = Azonal Impacted Degraded, TBE = Transitional Benchmark, TIG = Transitional Impacted Good Quality, TID = Transitional Impacted Degraded, ZBE = Zonal Benchmark, ZIG = Zonal Impacted Good Quality, and ZID = Zonal Impacted Degraded.

Discussion

Comparison of species richness

In general, the number of lemur species diminished considerably among habitats with increasing anthropogenic pressures. The presence of large remaining trees in a given habitat appears to play an important role in the maintenance of lemur species richness. For example, the Zonal Benchmark and Azonal Impacted Good Quality habitats, which still have many large trees, contained the highest species richness (10 species) of the eight forested habitats. The complete absence of lemurs in the Azonal Impacted Degraded habitat is presumed to be associated with the total lack of trees in this *Erica* bush area. Nonetheless, certain habitats that still hold some large trees, such as the Zonal Impacted Good Quality and Transitional Impacted Degraded habitats have reduced species richness (seven species). Clearly, other aspects enter into ecological

correlates associated with lemur species richness. Anthropogenic pressures in the Zonal Impacted Good Quality and Transitional Impacted Degraded habitats were notably high, which effect forest vegetation structure. Human hunting pressure for bushmeat, particularly for the larger diurnal species, may also be affecting lemur species richness within a given habitat type.

Our measure of species richness within the Ambatovy-Analamay forest was reduced as compared to previous studies in the region (Rapport Ambatovy, 2007, 2008) (see discussion below under "Biogeographic analysis"). A comparison of lemur species richness at several sites in the central eastern humid forests of Madagascar at mid-elevations and in close proximity to the Ambatovy-Analamay forest shows some interesting patterns. In total, 13 species of lemur have been verified from the Ambatovy-Analamay forest (present study; Rapport Ambatovy, 2007, 2008), which is just slightly less than the 14

species recorded in the Mantadia-Zahamena corridor (Schmid *et al.*, 1999) and from the Maromiza Forest (Rakotosamimanana *et al.*, 2004; Randrianambinina & Rasoloharijaona, 2006), and greater than the 12 species in the Réserve Spéciale d'Analamazaotra (Mittermeier *et al.*, 2006). Further, the Ambatovy-Analamay forest contains higher lemur species richness than the nine species known from the Anjozorobe-Angavo forested corridor (Ralison, 2007), which falls within a slightly higher elevational range and is located 50 km to the northwest of Ambatovy.

Biogeographic analysis

To place the lemur fauna of the Ambatovy-Analamay forest in a greater biogeographic context, a faunal analysis was conducted to compare species assemblages in this forest block with three sites in the central eastern mid-elevation forests (Mantadia-Zahamena, Analamazaotra, and Maromiza), as well as two zones in the Central Highlands (Ambohitantely and Anjozorobe-Angavo). The species of lemurs occurring in the Ambatovy-Analamay forest have broad distributions across the central eastern humid forests and the Central Highlands (Table 6). Using these data, Jaccard Indices were calculated for the lemur communities of these different forest blocks and the data matrix is presented in Table 7. The resulting dendrogram of faunal similarity is presented in Figure 5. Two distinct groupings are represented in the dendrogram. The first is composed of the Central Highland sites (Ambohitantely and the Anjozorobe-Angavo) and the second of the central eastern mid-elevation forests (Ambatovy-Analamay, Mantadia-Zahamena, Analamazaotra, and Maromiza). The distance associated with the split between these two groups is considerable, reflecting a notable difference in the lemur faunas of these two regions.

In order to clarify aspects of the distributions of certain lemur species, particularly with respect to previous lemur surveys in Ambatovy-Analamay forest, a few aspects need to be mentioned:

1. *Prolemur simus* – The recent discovery of *P. simus* in the Ambatovy forest was confined to the Totorofotsy marsh region (Dolch *et al.*, 2004). This species feeds extensively on the bamboo *Cathariostachys madagascariensis* (Tan, 1999), and its distribution is intimately tied to the non-continuous distribution of this plant (Rasoloarison & Rasolonandrasana, 1999; Goodman *et al.*, 2001; Wright *et al.*, 2008). This bamboo species was not found in any of the sites inventoried in early 2009.
2. *Lepilemur microdon* – This species was not recorded during the early 2009 inventories of the Ambatovy-Analamay forest, but was noted in earlier surveys of this zone. The taxonomy of the genus *Lepilemur* and the associated distribution of species has been the subject of numerous recent studies, mostly using molecular genetics (Andriaholinirina *et al.*, 2006). In some slightly older taxonomic treatments of this genus, two different non-sympatrically occurring forms were recognized by some specialists in the eastern humid forests -- *L. mustelinus* from 13°45' to 18°25'E and *L. microdon* from 18° to 24°50'S (e.g., Jenkins, 1987). The morphological differences between these forms are at best subtle and certainly difficult to discern based on field observations of free-living forest-dwelling animals. Other specialists considered *L. microdon* to be a synonym of *L. mustelinus* (e.g., Tattersall, 1982). In either case, the geographical limit of these two forms has been ambiguous and there are several published records of *L. microdon* in the central portion of the eastern humid forest. Recent molecular studies conducted to resolve this question have indeed found that the two taxa should be recognized, with the more lowland form from the Mantadia area being referable to *L. mustelinus* (Andriaholinirina *et al.*, 2006). Hence, the previous records of *L. microdon* in the Ambatovy-Analamay forest are unsubstantiated until further evidence from molecular studies is available.
3. *Cheirogaleus crossleyi* – This species was not observed during our early 2009 field studies in the Ambatovy-Analamay forest, although previous studies have suggested its local presence (Rapport Ambatovy, 2007, 2008). Based on studies of older museum specimens and morphological studies, Groves (2000) identified seven species of *Cheirogaleus*. One of these species, *C. crossleyi*, was identified from the Central Highlands and reputedly partially sympatric with *C. major*. In a large scale genetic and morphometric study of *Cheirogaleus* samples from across the island, Groeneveld *et al.* (2009) identified only three distinct taxa (*C. major*, *C. medius*, and *C. crossleyi*) and they placed the other four species recognized by Groves (2000) into synonymy. On the basis of the material they had access to, the form of *Cheirogaleus* occurring at Andasibe and Ranomafana (Ifanadiana) as well as at several Central Highland areas are *C. crossleyi*. Further,

Table 6. Measures of species richness, based on presence-absence data, in six different forests in the central portions of the eastern humid forests. 1 = species present, 0 = species absent. Ambat = Ambatovy-Analamay forest (nine sites between 980-1170 m), Amboh = Réserve Spéciale d'Ambohitantely (one site at 1500 m), MZ = Mantadia-Zahamena corridor (the site of Iofa at 960 m), Anala = Réserve Spéciale d'Analamazaotra (1200 m), Anjoz = Anjozorobe-Angavo forest corridor (one site at 1250 m), and Marom = Maromiza (1000 m). Bibliographic sources for data are presented in footnotes.

Species	Ambat	Amboh ^a	MZ ^b	Anala ^c	Anjoz ^d	Marom ^e
<i>Microcebus rufus</i>	0	1	1	0	1	0
<i>M. lehilahytsara</i>	1	0	0	1	1	1
<i>Allocebus trichotis</i>	1	0	0	1	0	1
<i>Cheirogaleus major</i>	1	0	1	1	0	1
<i>C. crossleyi</i>	1	1	0	1	1	0
<i>Lepilemur mustelinus</i>	1	0	1	1	1	1
<i>Hapalemur griseus</i>	1	0	1	1	1	1
<i>Prolemur simus</i>	1	0	0	0	0	1
<i>Eulemur rubriventer</i>	1	0	1	1	0	1
<i>E. fulvus</i>	1	1	1	1	1	1
<i>Varecia variegata</i>	1	0	1	0	0	1
<i>Avahi laniger</i>	1	1	1	1	1	1
<i>Propithecus diadema</i>	1	0	1	0	1	1
<i>Indri indri</i>	1	0	1	1	1	1
<i>Daubentonia madagascariensis</i>	1	0	0	1	0	1
TOTAL	14	4	10	11	9	13

^a Data herein.

^b Schmid *et al.* (1999).

^c Mittermeier *et al.* (2006).

^d Ralison (2007).

^e Rakotosamimanana *et al.* (2004).

they identified several Central Highland sites where *C. crossleyi* and *C. major* occur in sympatry. Hence, the coexistence of these two species in the Ambatovy-Analamay forest is possible, but molecular studies are needed to confirm this.

Table 7. Data matrix of Jaccard Index coefficients for lemur species composition in six different forests in the central portions of the eastern humid forest. Original presence-absence data are presented in Table 6. Two forests have approximately the same species if Jaccard Index coefficient is high. Ambat = Ambatovy-Analamay forest, Amboh = Réserve Spéciale d'Ambohitantely, MZ = Mantadia-Zahamena corridor, Anala = Réserve Spéciale d'Analamazaotra, Anjoz = Anjozorobe-Angavo forest corridor, and Marom = Maromiza.

	Ambat	Amboh	MZ	Anala	Anjoz
Amboh	0.20				
MZ	0.60	0.27			
Anala	0.78	0.25	0.50		
Anjoz	0.53	0.44	0.58	0.54	
Marom	0.93	0.13	0.64	0.71	0.47

Analysis of density

When calculating measures of lemur densities based on relatively rapid field inventories, several factors provide confounding aspects in the interpretation of the resulting estimates. These include, for example, aspects of weather patterns such as cyclonic periods,

rainfall, average minimum and maximum daily temperatures; the experience and competence of the observer(s); seasonality, as some lemurs undergo reduced activity during certain seasons; and chance aspects of where transects were installed in vegetational heterogeneous forest parcels. During our early 2009 inventories, strong rainfall occurred in Zonal Benchmark and Zonal Impacted Degraded (with an average rainfall of 33.9°C vs. less than 11.7°C in other habitats) associated with passing cyclonic systems, which may have considerably reduced lemur activities.

The notably high densities of *Microcebus lehilahytsara* in the Azonal Benchmark, Azonal Impacted Good Quality, and Zonal Impacted Good Quality habitats is presumed to be associated with the adaptability of members of this genus to forest degradation, particularly associated with vegetation structure, including understory structure and abundance of lianas, and food resources. It has already been noted that members of this genus are notably tolerant to habitat disturbance and often have higher densities between forest and forest edge habitats (Hladik *et al.*, 1980; Ganzhorn, 1995).

Allocebus trichotis was located in two habitat types, Azonal Impacted Good Quality and Transitional Benchmark, and its densities were relatively high in the latter habitat. Based on field observations, the

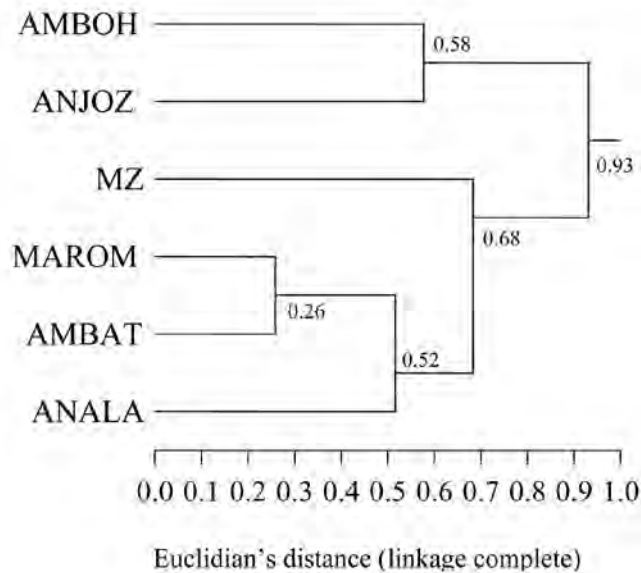


Figure 5. Branching diagram based on the Jaccard Index coefficients presented in Table 7. Ambat = Ambatovy-Analamay forest, Amboh = Réserve Spéciale d'Ambohitantely, MZ = Mantadia-Zahamena corridor, Anala = Réserve Spéciale d'Analamazaotra, Anjoz = Anjozorobe-Angavo forest corridor, and Marom = Maromiza.

distribution and abundance of this species appears to be associated with large trees remaining within a forested habitat, particularly *Uapaca* (Family Euphorbiaceae). An explanation of this relationship might be that *A. trichotis* uses the holes of *Uapaca* tree as sleeping sites.

The density of *Cheirogaleus major* was relatively high in habitats of relatively good quality (Azonal Impacted Good Quality, Transitional Impacted Good Quality, and Zonal Impacted Good Quality). This species uses the upper portions of large trees while searching for young leaves or leaf buds of saplings for food (Ganzhorn, 1988).

A comparison of the relative abundance measures of *Lepilemur mustelinus* and *Avahi laniger* seems to negatively co-vary between these taxa in certain habitats (Azonal Benchmark, Transitional Impacted Good Quality, Transitional Impacted Degraded, and Zonal Benchmark), which could be associated with competition for food resources (Ganzhorn, 1989). The sympatric occurrence of these two taxa is known from numerous localities in the eastern humid forests (e.g., Schmid *et al.*, 1999; Randrianambinina & Rasoloharijaona, 2006; Ralison, 2007).

For *Hapalemur griseus*, density was relatively low in the Azonal Benchmark habitat. Based on field observations, the considerable quantities of potential food and its broad local distribution are suggested as the reasons this lemur had high densities in the Azonal Impacted Good Quality and Transitional Impacted Degraded habitats. It is important to mention that the narrow dietary requirements of this species associated

with young bamboo sprouts and grasses, result in considerable horizontal displacement associated with locating food resources (Overdorff, 1996), which are not equally distributed within a forest.

For the other diurnal lemurs, numerous species were present in the Ambatovy-Analamay forest, but not in relatively high densities. At sites where at least three diurnal species were recorded (Azonal Benchmark, Transitional Impacted Good Quality, and Zonal Benchmark), there was no notable difference in their densities. In contrast, at sites with two diurnal species (Transitional Impacted Degraded and Zonal Impacted Good Quality), there was always one taxon that had notably higher densities than the other. The reduced densities of certain diurnal lemur species in the Zonal Benchmark and Zonal Impacted Degraded habitats is probably associated with human pressures, such as forest usage for cattle pasture and selective logging of large trees. Further, the diurnal species found in these habitats were notably shy in the presence of humans, which may also be associated with hunting pressure.

Lemur densities calculated in this survey were notably high as compared to those obtained in the same area by other researchers (Rapport Ambatovy, 2007, 2008) or densities for nearby localities, such as the Mantadia or Maromiza forests. Several explanations can be offered to explain these differences. In our early 2009 study, transect lines were relatively short, which might have an impact on a reduced tendency of the observer losing concentration as compared to long transects. Further, a single long transect line in a

given forest block, as compared to a series of shorter ones, might not pass through as many different local habitats. Furthermore, numerous other natural history parameters might explain differences between the research groups in their density estimates, such as seasonality, food availability, resource dispersion, or explicitly the installation of mine infrastructure. Notable levels of vegetational variation have been documented in eastern humid forests of Madagascar, including the region of Andasibe (Abraham *et al.*, 1996), which can have considerable impact on variation of lemur densities in the same forest block, depending in part on where the transects are placed. Finally, repeated transect sampling for primates in eastern humid forests does not produce data suitable for distance sampling analysis and these data cannot be used as a baseline for ecological monitoring (Hawkins *et al.*, 2006).

Conclusion

Twelve different species of lemur were identified in the Ambatovy-Analamay forest during inventories conducted in the early portion of 2009 in nine different habitat types. Generally, lemur species richness declines with the level of habitat degradation or in other words, lemur species richness is highest in habitats that retain large trees. Further, other factors (climatic and anthropogenic) have an impact on lemur density in the different habitats. In a regional sense, the Ambatovy-Analamay forest has a roughly equivalent level of species richness as nearby forested areas at approximately the same elevation.

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