



Effects of Transect Selection and Seasonality on Lemur Density Estimates in Southeastern Madagascar

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I investigated how transect type (trails vs. cut transects) and seasonality influenced density estimates for 5 lemur taxa (Avahi laniger, Cheirogaleus major, Eulemur rubriventer, Hapalemur griseus griseus, and Microcebus rufus) in the Vohibola III Classified Forest in SE Madagascar. I surveyed tree height and diameter and lemur populations from June 1 to December 28, 2004 along 2 1250-m trails local people used and 2 1250-m transects cut parallel to the trails in primary rain forest. Despite dendrometric variations within and between trails and transects, only density estimates of Hapalemur griseus griseus differed significantly by transect type. The spatial variation may be a result of removal by local people of giant bamboo, which is the main food for Hapalemur griseus griseus, along trails. Conversely, seasonality influenced density estimates for Cheirogaleus major, Eulemur rubriventer, Hapalemur griseus griseus, and Microcebus rufus. The temporal variations may be related to seasonal torpor for Cheirogaleus major and increased detection probabilities during periods of fruit exploitation for Eulemur rubriventer, Microcebus rufus, and Hapalemur griseus griseus. Transect type and seasonality did not affect density estimates for Avahi laniger, which may be related to the highly folivorous and low-energy diet of the nocturnal lemur. Researchers surveying lemurs along line transects should be aware that transect selection may influence density estimates for Hapalemur griseus griseus and that seasonality may influence density estimates for Cheirogaleus

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major, *Eulemur rubriventer*, *Hapalemur griseus griseus*, and *Microcebus rufus*.

KEY WORDS: density estimates; frugivory; lemurs; randomization; surveys.

INTRODUCTION

Line-transect surveys are an important tool for assessing specific presence-absence, community structure, and density estimates in tropical mammals (Buckland *et al.*, 2001; Rodrigues *et al.*, 2000). Studies of primate conservation biology and community ecology also widely use density estimates from the surveys (Ganzhorn *et al.*, 1999; Jernvall and Wright, 1998; Reed, 1999). For example, Reed (1999) found that the density of even 1 species is important in determining the overall ecological space a lemur community exploits. Despite considerable discussion of the assumptions necessary for using surveys to determine accurate density estimates and the various methods to determine density (Buckland *et al.*, 2001; Fashing and Cords, 2000; Peres, 1999; Whitesides *et al.*, 1988), there are few data on how transect selection and seasonality influence primate density estimates. Therefore, understanding how spatial and temporal factors influence species-specific density estimates is important for many fields of primate research.

Though Buckland *et al.* (2001) advocated random selection of transect locations, some studies require selection of specific locations to ensure inclusion of important environmental response variables (Peres, 1999). For example, researchers studying the effects of forest edges on mammal ecology typically set up transects perpendicular to the forest edge (Lehman *et al.*, 2006a). Conversely, researchers analyzing primate responses to hunting and logging tend to set up their transects in forests experiencing different intensities of each anthropogenic factor (Chapman *et al.*, 2000; Paciulli, 2004; Peres and Dolman, 2000). Researchers have typically combined survey data from both trails and cut transects to determine lemur sighting rates or density estimates, or both (Johnson and Overdorff, 1999; Lehman, 2000; Rakotondravony and Razafindramahatra, 2004). However, there are few data on variations in lemur density estimates between trails local people use and transects cut in primary forests (*cf.* *Eulemur fulvus*; Johnson and Overdorff, 1999).

Seasonality is an important factor influencing lemur evolutionary ecology (Ganzhorn *et al.*, 1999; Lehman *et al.*, 2005; Wright, 1999). The austral summer (*ca.* May–August) is associated with low ambient temperatures and rainfall as well as resource scarcity for many lemurs (Wright, 1999). Thus, there are seasonal variations in lemur activity patterns (Atsalis,

1999b; Lemelin and Schmitt, 2004; Overdorff *et al.*, 1997). For example, female *Microcebus rufus* have reduced activity periods and may undergo seasonal torpor during June–August in SE Madagascar (Atsalis, 1999b; Randrianambinina *et al.*, 2003). *Cheirogaleus major* enter a torpor period between May and mid-August (Petter *et al.*, 1977; Wright and Martin, 1995). Therefore, the question arises if seasonality influences lemur density estimates.

My objective was to determine how transect location and seasonality influence density estimates for 5 lemur taxa (*Avahi laniger*, *Cheirogaleus major*, *Eulemur rubriventer*, *Haplemur griseus griseus*, and *Microcebus rufus*) in the Vohibola III Classified Forest in SE Madagascar. Specifically, I sought to answer the questions: 1) Do species-specific lemur density estimates differ between surveys along trails that local people use and those conducted along transects cut in primary forest? 2) Do species-specific lemur density estimates differ between surveys conducted in June–August and surveys conducted in October–December?

METHODS

I collected data from June 1 to December 28, 2004 at Camp Mangatsiaka in the Vohibola III Classified Forest. Vohibola III is a 2034-ha forest fragment at 20°43'S and 47°25'E, 200 km SE of the capital city of Antananarivo and 40 km north of RNP (Ranomafana National Park; Fig. 1). Camp Mangatsiaka is at 20°41'32"S, 47°26'15"E (1180 m altitude) in the central section of Vohibola III. Rainfall amounts average 2478 mm per year, and the heaviest rains tend to come during the December to March warm, wet season (Lehman, unpublished data). The average annual temperature is $20.2 \pm 3.5^\circ\text{C}$, with annual lows (4°C) in May–June.

Vohibola III is in the mid-altitude humid forest region of SE Madagascar (Nicoll and Langrand, 1989). Forests in Vohibola III predominantly comprise endemic species of *Tambourissa* (Monimiaceae), *Ehippiandra* (Monimiaceae), *Ocotea* (Lauraceae), *Breonia* (Rubiaceae), *Oncostemum* (Myrsinaceae), and *Cyathea* (Cyatheaceae). The shrub and herb layers include various species of Compositae, Rubiaceae, and Myrsinaceae. A high diversity of *Pandanus* species (Pandanaeae), bamboos (Poaceae), and epiphytic plants also exists. The canopy is continuous and averages 12 m in height, and the tallest trees are 25 m in height (Lehman *et al.*, 2006a).

I sighted 4 nocturnal lemur taxa (*Avahi laniger*, *Cheirogaleus major*, *Lepilemur mustelinus*, and *Microcebus rufus*) and 4 diurnal/cathemeral lemur taxa (*Eulemur rubriventer*, *E. fulvus rufus*, *Haplemur griseus griseus*, and *Propithecus diadema edwardsi*) in Vohibola III (Lehman *et al.*,

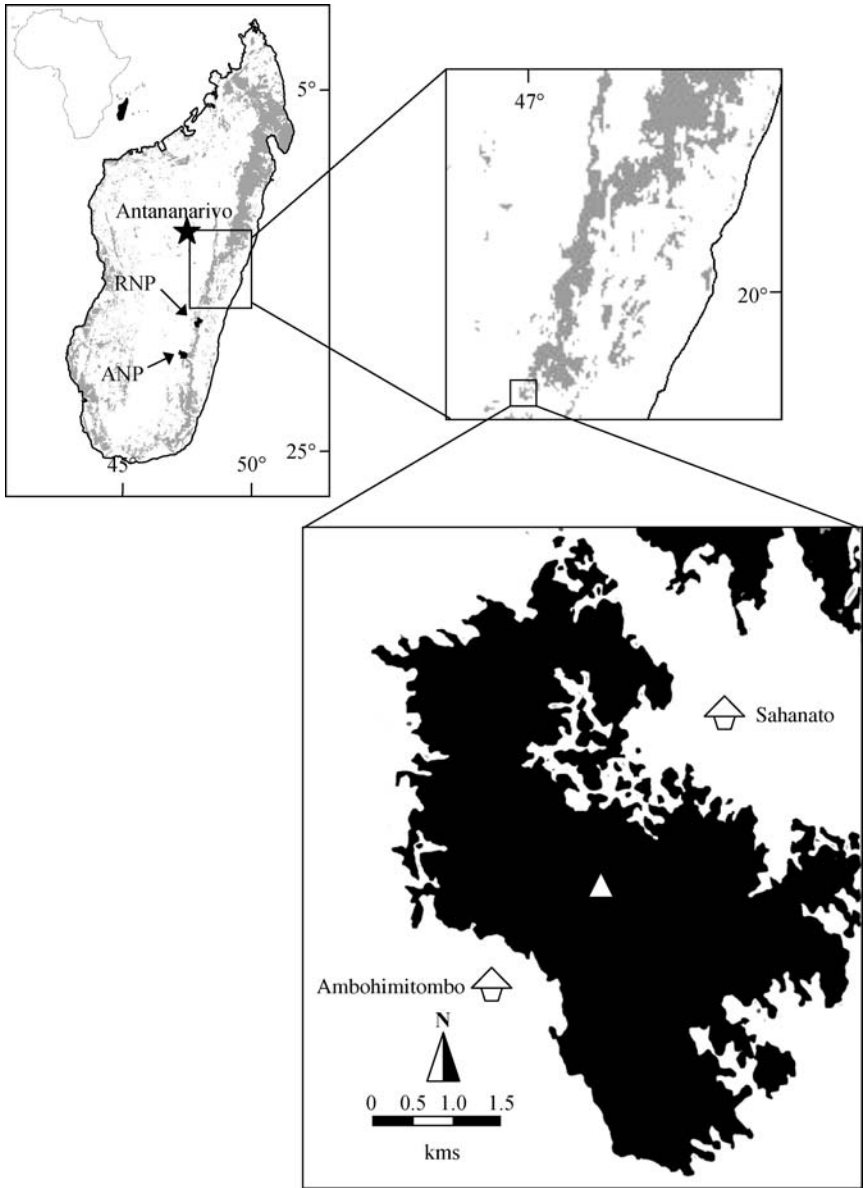


Fig. 1. Location of Vohibola III Classified Forest, Ranomafana National Park (RNP), and Andringitra National Park (ANP). Triangle indicates location of Camp Mangatsiaka.

2006a). Bite marks on tree branches and trunks indicated the possible presence of *Daubentonia madagascariensis* in Vohibola III; however, I did not sight one. Hunting by local people in the fragment and other nearby forests may have extirpated *Varecia variegata variegata* (Lehman *et al.*, 2006b). However, hunting pressures and anthropogenic disturbances have been low since the 2003 designation of Vohibola III as a Classified Forest (Lehman *et al.*, 2006b).

I conducted botanical and lemur surveys along 4 1250-m transects in Vohibola III. Two of the transects (T1 and T2) were along trails local people used to travel through the forest and selectively log trees for use as firewood, housing materials, medicine, and carving material. My assistants and I cut each of the other transects (C1 and C2) in primary forest parallel to and 250 m away from T1 and T2. Each transect ran perpendicular to the forest edge as part of a longitudinal study of edge effects and their influence on lemur and forest ecology (Lehman *et al.*, 2006a). I used numbered flagging tape to mark 10-m increments along each trail and cut transect. I conducted botanical surveys along both sides of each trail and transect to a depth of 1 m, for a total area sampled of 1 ha. I collected data on height (m) and dbh (diameter at breast height, cm) for all trees >10 cm dbh. I then compared dendrometric data for Vohibola III to similar data collected at RNP and ANP (Andringitra National Park; Balko and Underwood, 2005; Johnson, 2004; Johnson and Overdorff, 1999). I chose the sites because they are the closest protected areas to Vohibola III, have broadly similar habitat types, and contain the same lemur taxa.

I walked trails and cut transects slowly (0.5–1.0 km/h) during times of the day (0700–1100 h and 1400–1700 h) and night (1900–2230 h) best suited for locating lemurs. I rotated starting points for all surveys to prevent bias and collected the following data: date, time of sighting, trail/transect number, participants, perpendicular distance from trail to first individual seen/middle of group, species/subspecies, group composition and size, height (m) of first individual seen, group spread, and method of detection. I used specific and subspecific characteristics in Mittermeier *et al.* (1994) and Garbut (1999) for field identification. I captured no lemur.

I used χ^2 tests to determine if there were significant differences in the number of stems between transects as well as differences in survey effort for diurnal surveys and nocturnal surveys between transect types and seasons. *A priori* analyses via a Levene test at $p < 0.05$ indicated unequal variances for tree height and dbh on each trail and transect. Thus, I used nonparametric tests to determine dendrometric variations within (Mann-Whitney *U* tests) and between (Kruskal-Wallis tests) trails and transects. I conducted the tests via SPSS 11.5.

Density estimates are only for the 5 lemur taxa with a minimum of 90 individual sightings for solitary species (*Avahi laniger*, *Cheirogaleus major*, and *Microcebus rufus*) and 60 group sightings for group-living species during the survey period (*Eulemur rubriventer* and *Hapalemur griseus griseus*). I chose the values because of issues with low sample sizes in computing density estimates (Buckland *et al.*, 2001). I computed lemur densities (no. of individuals/km²) by dividing the number of individuals surveyed by the total survey area (Whitesides *et al.*, 1988). I estimated species-specific sighting widths for each transect via the perpendicular distance (m) from the individual (for solitary taxa) or center of the group (for group-living taxa) to the transect and the histogram inspection technique, with a 50% criterion for falloff distance. I did not include infants in group counts. I computed standard deviations for density estimates by using each transect sample separately.

I used a 2-sample randomization test with 1000 iterations to determine if there were intraspecific differences in 1) perpendicular sighting distances between transect types (trails and cut transects), 2) perpendicular sighting distances between seasons (June–August and October–December), 3) density estimates between trails and cut transects, and 4) density estimates between seasons. Randomization requires no assumption regarding the underlying distribution of the data—an issue with density estimates for group-living taxa—and is applicable to small sample sizes (Fortin and Dale, 2005). I report only significance values (p) because randomization tests do not produce a statistical test value. I computed randomization tests via the PopTools add-in for Microsoft Excel (Hood, 2004). All statistical tests are 2-tailed, and I set the α level at 0.05.

RESULTS

Habitat characteristics and dendrometric data for Vohibola III, RNP, and ANP are in Table I. There is no significant difference in the number of stems per transect between T1 and T2 ($\chi^2 = 0.75$, $df = 1$, $p = 0.39$) or between C1 and C2 ($\chi^2 = 3.05$, $df = 1$, $p = 0.08$). However, the number of stems is significantly lower on trails than on transects ($\chi^2 = 141.3$, $df = 1$, $p = 0.0001$). There are significant variations in tree height ($U = 6957.0$, $z = -8.89$, $p = 0.0001$) but not dbh ($U = 14650.5$, $z = -1.06$, $p = 0.288$) between T1 and T2. Tree height ($U = 67390.0$, $z = -10.32$, $p = 0.0001$) and dbh ($U = 99713.0$, $z = -2.82$, $p = 0.005$) are significantly higher on C2 than on C1. Moreover, there are variations in tree height ($H = 197.84$, $df = 3$, $p = 0.0001$) and dbh ($H = 34.66$, $df = 3$, $p = 0.0001$) across all trails and transects in Vohibola III. Mean tree height is lower, particularly for T2 and C1,

Table 1. Habitat characteristics and dendrometric data for Vohibola III, Ranomafana National Park, and Andringitra National Park in SE Madagascar

Site	Location	Disturbance	Elevation (m)	Plot size (m ²)	N stems per plot	Mean height (m)	Mean dbh (cm)	Source ^a
Vohibola III	T1	SL	1217	2500	190	12.6	19.4	1
	T2	SL	1212	2500	165	9.1	19.5	1
Ranomafana	C1	UL	1108	2500	513	10.8	16.6	1
	C2	UL	1126	2500	435	13.3	17.9	1
	Vatoharanana	SL	1100	—	—	15.0	31.2	2
	Talatekely	HL	1030	—	—	13.2	19.7	2
Andringitra	Valohoaka	UL	1200	—	—	14.8	29.3	2
	Ambarongy	UL	700–900	625	65	20.0	16.8	3
	Ambarongy	UL	700–900	625	30	20.7	27.6	3
	Ambarongy	UL	700–900	625	59	19.6	18.9	3
	Ambarongy	UL	700–900	625	71	21.9	21.6	3
	Parc	UL	800	625	79	13.2	15.5	3
	Parc	UL	800	625	69	13.2	15.8	3

Note. — means no datum available. SL = selectively logged; UL = unlogged; HL = heavily logged.

^a1 = Present study; 2 = Balko and Underwood (2005); 3 = Johnson (2004).

Table II. Frequency distribution of lemur surveys conducted along trails and cut transects in Vohibola III

Number	Description	Survey frequency		
		Diurnal	Nocturnal	Total
T1	Trail	92	34	126
T2	Trail	77	33	110
C1	Cut transect	85	33	118
C2	Cut transect	94	34	128
Total		348	134	482

in Vohibola III compared to plots in RNP and ANP. Mean dbh is higher for trails in Vohibola III compared to 2 Ambarongy and 2 Parc locations whereas mean dbh along transects is higher only than the Parc locations in ANP.

I conducted a combined total of 482 diurnal ($N = 348$) and nocturnal ($N = 134$) lemur surveys in Vohibola III (Table II). There is no significant difference in the distribution of diurnal surveys ($\chi^2 = 0.01$, $df = 1$, $p = 0.90$) or nocturnal surveys ($\chi^2 = 0.01$, $df = 1$, $p = 0.99$) between trails and cut transects. Moreover, survey frequencies did not differ between seasons for either diurnal ($\chi^2 = 1.07$, $df = 1$, $p = 0.30$) or nocturnal surveys ($\chi^2 = 1.70$, $df = 1$, $p = 0.19$). There is also no difference in species-specific perpendicular detection distances between trails and cut transects (Table III) or between seasons (Table IV). Thus, my data are not an artifact of differential detection probabilities between habitats or seasons.

There is no significant difference in density estimates between trails and cut transects for *Avahi laniger*, *Cheirogaleus major*, *Eulemur rubriventer*, and *Microcebus rufus* (Table V). For *Hapalemur griseus griseus*, the mean density estimate for trails is significantly lower than that for cut transects. I combined survey data collected on trails and cut transects for

Table III. Comparison of mean perpendicular sighting distances for lemurs surveyed along trails and cut transects in Vohibola III

Species	Mean perpendicular distance (m) \pm 1 SD				
	Trails	N	Cut transects	N	P
<i>Avahi laniger</i>	8.37 \pm 6.81	55	5.20 \pm 3.25	49	.134
<i>Cheirogaleus major</i>	5.60 \pm 2.77	60	5.70 \pm 2.99	36	.789
<i>Eulemur rubriventer</i>	10.26 \pm 8.62	66	8.61 \pm 1.02	54	.571
<i>Hapalemur griseus griseus</i>	7.44 \pm 4.03	11	6.75 \pm 4.50	49	.568
<i>Microcebus rufus</i>	4.08 \pm 2.18	80	4.81 \pm 3.67	77	.871

Note. N refers to number of individuals sighted for solitary species and number of groups sighted for group-living species.

Table IV. Comparison of mean perpendicular sighting distances for lemurs surveyed during 2 time periods (June–August and October–December) in Vohibola III

Species	Mean perpendicular distance (m) ± 1 SD				
	June–August	N	October–December	N	P
<i>Avahi laniger</i>	8.76 ± 7.16	43	5.53 ± 4.36	27	.253
<i>Cheirogaleus major</i> ^a	—	0	5.48 ± 2.92	88	—
<i>Eulemur rubriventer</i>	10.02 ± 7.79	40	7.88 ± 4.74	45	.740
<i>Haplemur griseus griseus</i>	7.04 ± 4.89	30	5.33 ± 3.37	11	.631
<i>Microcebus rufus</i>	4.77 ± 3.68	66	3.87 ± 1.88	70	.587

Note. N refers to number of individuals sighted for solitary species and number of groups sighted for group-living species. Sample sizes differ from those in Table III because of removal of data for September.

^aSighted only during September–December.

all lemur taxa except *Haplemur griseus griseus* (Table V). I analyzed temporal variations in density estimates for *Haplemur griseus griseus* only for cut transects because of significant spatial effects and low sample sizes for trails. There is no significant difference in mean density estimates between June–August and October–December for *Avahi laniger*. I did not sight *Cheirogaleus major* in June–August. Density estimates are significantly lower during June–August than in October–December for *Eulemur rubriventer* and *Microcebus rufus*. Conversely, *Haplemur griseus griseus* density estimates are significantly higher during June–August than in October–December.

DISCUSSION

There are clear anthropogenic effects on habitat characteristics between trails and transects in Vohibola III. For example, there were fewer stems along trails compared to transects, which was the result of local people selectively removing trees along the trails. Though the numbers of stems and dbh were similar between trails, mean tree height was higher for T1 (12.6 m) than for T2 (9.1 m). Local people tended to harvest tall trees from T2 for use as firewood in production of illegal rum ≤ 100 m of the forest edge. Conversely, local people transported shorter trees from T1 for use as firewood and housing materials to the nearby (ca. 1.5 km from forest edge) village of Sahanato. Local people rarely transport wood from Vohibola III to Ambohitombo because they must cross a large river, which lacks a bridge, to reach the village. However, mean tree height along transects cut in primary forests were also lower than most sites in RNP and ANP. The dendrometric variations may in part be the result

Table V. Comparisons of mean lemur density estimates (number individuals/km² ± 1 SD) between trails and cut transects as well as between time periods (June–August and October–December) in Vohibola III

Species	Trails	Cut transects	<i>p</i>	June–August	October–December	<i>p</i>
<i>Avahi laniger</i>	23.88 ± 7.91	17.91 ± 15.35	0.33	15.05 ± 9.71	18.33 ± 12.83	.67
<i>Chetrogaleus major</i>	70.07 ± 47.93	66.67 ± 34.57	0.47	—	56.67 ± 28.43	NA
<i>Eulemur rubriventer</i>	21.64 ± 2.18	21.43 ± 4.19	0.97	13.95 ± 1.32	21.83 ± 6.05	.02
<i>Hapalemur griseus griseus</i>	4.84 ± 0.96	14.09 ± 1.88	0.03	10.35 ± 2.91	3.25 ± 1.91	.001
<i>Microcebus rufus</i>	46.27 ± 11.53	49.25 ± 13.86	0.47	40.02 ± 0.49	64.58 ± 11.36	.03

Note. Sample sizes are listed in Tables III and IV. NA refers to not applicable for statistical comparisons due to seasonal torpor in *C. major*.

of the inclusion of trees from edge habitats in Vohibola III. Tree height and dbh are negatively influenced by edge proximity in SE Madagascar (Lehman *et al.*, 2006a; Lehtinen *et al.*, 2003) and at other forest sites (Ries *et al.*, 2004). The botanical plots in RNP and ANP were not close to forest edges, except possibly for the Talatekely site. Moreover, methodological differences existed in botanical sampling between each study, which can further complicate habitat comparisons. For example, I used 2 m × 1250 m botanical transects whereas Balko and Underwood (2005) employed a point-center-quarter method. Thus, specific correlates to intersite variations in forest structure reflect complex and regionally varying causalities that cannot be analyzed fully via the data available at present.

My first question was to determine if there are differences in lemur density estimates between surveys along trails that experienced selective logging by local people compared to transects cut in primary forests. Despite variations in dendrometrics between trails and transects, there is no difference in perpendicular sightings distances or spatial variations in density estimates for *Avahi laniger*, *Cheirogaleus major*, *Eulemur rubriventer*, or *Microcebus rufus*. Lack of a density response to dendrometric variations might be expected because the 4 taxa are among the most abundant and widespread of all lemurs (Irwin *et al.*, 2005; Lehman, 2006; Mittermeier *et al.*, 1994) and they tend to be abundant at sites that have experienced selective logging (Atsalis, 1999a; Ganzhorn, 1995; Irwin *et al.*, 2000b; Lehman and Wright, 2000; Wright and Martin, 1995). Conversely, more patchily distributed taxa, such as *Propithecus diadema edwardsi* and *Varecia variegata variegata*, are sensitive to selective logging and hunting pressures (Arrigo-Nelson, 2005; Balko and Underwood, 2005; Britt, 2000; Irwin *et al.*, 2005; Lehman, 2006; Lehman *et al.*, 2006b; Ratsimbazafy, 2002).

Density estimates differ between trails and cut transects only for *Hapalemur griseus griseus*. Specifically, density estimates for the species are almost 3 times lower along trails compared to cut transects. I suggest that the low density estimates are a result of local people removing giant bamboo (*Cathariostachys madagascariensis* Poaceae)—which comprises 72% of the total annual diet of the lemur (Tan, 1999)—from trails in Vohibola III. Local people harvest giant bamboo for use as housing materials, e.g., roofing, walls to house livestock. Despite giant bamboo being common in primary forest, it is not present along any of the trails in Vohibola III (Lehman, unpublished data). Local people have started to collect bamboo in primary forest, which may have a detrimental effect on the long-term population dynamics of *Hapalemur griseus griseus*. It is important to note that *Hapalemur griseus griseus* consumes other types of woody bamboo, e.g., *Cephalostachyum viguieri* and *Cephalostachyum perrieri*, and that some populations live in areas where there is no

bamboo (Tan, *pers. comm.*). Hunting of *Hapalemur griseus griseus* by local people may also relate to reduced density estimates along trails in Vohibola III. Local people reported that in the past they had opportunistically hunted *Hapalemur griseus griseus*, but targeted larger-bodied species such as *Eulemur fulvus rufus* and *Propithecus diadema edwardsi* (Lehman *et al.*, 2006b). Hunting can reduce densities and group sizes of target species (Peres, 2000), and is cited as a major influence on primate socioecology and population dynamics (Goodman, 2003; Kappeler and van Schaik, 2002). If hunting had influenced *Hapalemur griseus griseus* along trails, then there should have been concomitant density variations for *Eulemur rubriventer*, which local people also hunt. However, there is no difference in density estimates between trails and cut transects for *Eulemur rubriventer*. Arrigo-Nelson and Wright (2004), Overdorff *et al.* (1997), Rakotondravony and Razafindramahatra (2004), and Wright *et al.* (1987) reported similar results for conspecifics in RNP. For example, Arrigo-Nelson and Wright (2004) found *Hapalemur griseus griseus* at sites where local people hunted lemurs. Thus, removal of giant bamboo rather than hunting pressure by local people relates to differences in density estimates for *Hapalemur griseus griseus* between trails and cut transects.

The effects of transect selection on density estimates for *Hapalemur griseus griseus* have important implications for studies of congeners, including the critically endangered *Hapalemur simus* and *H. aureus*. The issue exists because of similarities in behavioral ecology among *Hapalemur griseus griseus*, *H. simus*, and *H. aureus* (Tan, 1999). Density estimates are critical for setting conservation priorities (IUCN, 2004). Therefore, studies are needed to determine if density estimates for *Hapalemur simus* and *H. aureus* differ between trails and cut transects.

Density estimates for *Cheirogaleus major*, *Eulemur rubriventer*, *Hapalemur griseus griseus* (cut transects only), and *Microcebus rufus* differ between seasons in Vohibola III. Seasonal differences in sightings of *Cheirogaleus major* occurred because they undergo torpor during May to mid-September in SE Madagascar (Wright and Martin, 1995). Seasonal variations in density estimates for *Eulemur rubriventer*, *Microcebus rufus*, and *Hapalemur griseus griseus* reflect patterns of fruit exploitation. Fruit comprises 80% of the annual diet of *Eulemur rubriventer* (Overdorff, 1993). Overdorff (1993) found that in *Eulemur rubriventer*, the number of fruit patches visited and the average daily path length were higher during October–December than during June–August. *Microcebus rufus* also consumes fruit, with 75% of fecal remains containing seeds from fruiting trees (Atsalis, 1999a). Atsalis (1999a) documented that fruit consumption was higher during October–December than during June–August. Moreover, seasonal torpor may reduce the number of active and observable female *Microcebus rufus* during June–August (Atsalis, 1999b; Randrianambinina

et al., 2003). Though *Hapalemur griseus griseus* is a dietary specialist on bamboo, fruit comprises 5–15% of its total annual diet (Grassi, 2002; Tan, 2000). *Hapalemur griseus griseus* frugivory is generally most common during the cool dry season (May–August), which coincides with the time period of higher density estimates I observed in Vohibola III. Thus, I suggest that seasonal differences in detecting *Eulemur rubriventer*, *Microcebus rufus*, and *Hapalemur griseus griseus* occurred because the lemurs are more active and easily visible during time periods of fruit exploitation.

Density estimates are unaffected by transect type or seasonality only for *Avahi laniger*. Preliminary studies indicate that young leaves comprise 98% of the May–August diet of *Avahi laniger* in SE Madagascar (Faulkner and Lehman, 2005). The nocturnal species spends most of each night resting, which is adaptive for digestion and energy conservation (Ganzhorn *et al.*, 1985; Harcourt, 1991). For example, all sightings I made of them were of individuals resting in trees in Vohibola III. Although temperature tends to covary with availability of new leaves in SE Madagascar (Hemingway, 1998; Overdorff, 1993), it is difficult to determine how seasonality could affect density estimates for such a folivorous species. Further, there is no evidence that *Avahi laniger* switches to other food types, such as fruit, or enters torpor during periods of leaf scarcity. Thus, density estimates for *Avahi laniger* may not be influenced by transect type or seasonality because this species spends much of its time resting.

We need data on temporal patterns of fruit availability in Vohibola III because fruiting patterns vary seasonally and geographically in the eastern humid forests of Madagascar (Ganzhorn *et al.*, 1999; Johnson, 2004; Overdorff, 1996). Ganzhorn *et al.* (1999) observed that fruit availability is highly unpredictable in eastern Madagascar, in that fruit trees bear fruit approximately once every 3 yr. Johnson (2004) noted different temporal patterns of fruit production between ANP and RNP, which are only 115 km apart in SE Madagascar. Specifically, fruit production was highest from December to May in ANP and July–December in RNP. Thus, suggestions of a link between seasonal density estimates and fruit abundance should be viewed with caution pending site-specific data on phenology. Moreover, it is important to determine if the spatial and temporal patterns I documented for lemurs in Vohibola III are applicable to conspecifics and congeners at other sites in eastern humid forests.

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