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Edge Effects on the Density of *Cheirogaleus major*

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We investigated how greater dwarf lemur (Cheirogaleus major) *densities, ambient air temperature, and dendrometrics (tree height and diameter) varied along forest edge-interior gradients in the Vohibola III Classified Forest in SE Madagascar. We also assessed if spatial variations in densities of* Cheirogaleus major *provide indirect evidence of increased predation pressure in the transition zone between edge and interior forest habitats, i.e., an ecological trap. We conducted diurnal temperature surveys* ($N = 394$) *and nocturnal surveys of* Cheirogaleus major ($N = 182$) *over 2 yr along 4 1250-m transects that ran perpendicular to the forest edge in Vohibola III. We did not see* Cheirogaleus major *from May to mid-September, and the highest sighting frequency occurred during October–November.* Cheirogaleus major *exhibited a negative edge response because densities ranged from low levels in edge habitats to higher levels in the forest interior. After we tested for spatial autocorrelation, edge-related variations in densities of* Cheirogaleus major *covaried most strongly with tree diameter. Edge responses of* Cheirogaleus major *may reflect spatial variations in fruit and liana abundance, though data are needed on the precise relationship between tree diameter and food production to confirm the relationship. Edge-related variations in densities of* Cheirogaleus major *may also provide indirect evidence of an ecological trap. Testing and controlling for spatial autocorrelation should be important components of future studies of primate conservation biology and ecology.*

KEY WORDS: edge effects; fruit abundance; lemurs; madagascar; predation; spatial autocorrelation.

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INTRODUCTION

Edge effects represent the penetration, to varying depths and magnitudes, of abiotic and biotic conditions from the surrounding environment (matrix) into the forest interior (Chen *et al.*, 1992). Field research has revealed that edge effects can lead to the degradation of forest fragments (Laurance *et al.*, 2002). Edge effects may be particularly relevant to lemurs (Lehman *et al.*, 2006a,b), which are one of the most threatened mammalian taxa in the world owing to the loss of 80%–90% of forest habitats (Du Puy and Moat, 1998; Green and Sussman, 1990). The remaining forest is highly fragmented and, therefore, may be prone to extreme edge effects (Lehtinen *et al.*, 2003; Watson *et al.*, 2004). However, there are few data on how edge effects influence nocturnal lemurs, such as the greater dwarf lemur (*Cheirogaleus major*).

Cheirogaleus major is a small-bodied (362–436 g) lemur that tends to live in primary and well-established secondary humid forests in eastern Madagascar (Groves, 2000; Petter *et al.*, 1977; Smith and Jungers, 1997; Wright and Martin, 1995). Wright and Martin (1995) observed *Cheirogaleus major* eating fruit (86% of 158 feeding scores) and flowers/nectar (11% of 158 feeding scores) in Ranomafana National Park. *Cheirogaleus major* has the ability to store fat in its tail (Petter *et al.*, 1977). Petter *et al.* (1977) suggested and Wright and Martin (1995) confirmed that *Cheirogaleus major* retreat to tree holes during the Austral summer (*ca*. May–August), when food tends to be scarce. It is likely that *Cheirogaleus major* and congenera undergo hibernation—metabolic inhibition and reductions of body temperate to maximize energy conservation (Geiser and Ruf, 1995)—instead of torpor (Dausmann *et al.*, 2005). Moreover, hibernation typically involves longer time periods than torpor. Because *Cheirogaleus major* experiences a shortened annual activity period, it may be more susceptible to anthropogenic disturbances, such as edge effects, that alter food availability and abundance. Therefore, determining how *Cheirogaleus major* responds to edge effects can provide critical information to understand their ecology.

Lehman *et al.* (2006a) found that *Cheirogaleus major* were more abundant in interior than in edge habitats. However, we were unable to test for clinal variations in densities of *Cheirogaleus major* and ecological correlates to these patterns. If *Cheirogaleus major* responds negatively to edge effects, then this response may reflect clinal variations in abiotic edge effects (temperature) or biotic edge effects (food abundance, predation pressures) or both. Heightened ambient air temperatures tend to occur near forest edges (Gehlhausen *et al.*, 2000; Laurance *et al.*, 1997; Lehtinen *et al.*, 2003; Malcolm, 1998; Saunders *et al.*, 1999), which may inhibit *Cheirogaleus major* from achieving hibernation in these habitats. The hypothesis is based on a study by Ganzhorn and Schmid (1998) in which *Microcebus murinus* were unable to achieve torpor owing to heightened ambient temperatures near secondary habitats. Moreover, Dausmann *et al.* (2005) found that properties of the tree hole—tree height and wall thickness—influenced body temperature during hibernation in the fat-tailed dwarf lemur (*Cheirogaleus medius*). Poorly insulated tree holes resulted in body temperature fluctuations whereas well-insulated tree holes allowed a fairly constant body temperature. If tree height covaries negatively with edge proximity, then edge effects may be particularly relevant to the ecology of *Cheirogaleus major*.

Distribution patterns of *Cheirogaleus major* may also be influenced by edge-related variations in the abundance of fruits and lianas. Fruit and liana abundance tend to correlate positively with diameter at breast height (dbh) in the tropics (Chapman *et al.*, 1992; Leighton and Leighton, 1982; Stevenson, 2001; Zurring *et al.*, 1993), though the precise relationship between the variables is arguable (Ganzhorn *et al.*, 1999; Janson and Chapman, 1999). Thus, correlations between densities of *Cheirogaleus major* and tree diameter may reflect edge-related variations in feeding ecology. Finally, there may be edge-related variation in predation pressures, which Schlaepfer *et al.* (2002) have referred to as an ecological trap. An ecological trap occurs when habitat disturbance alters environments and then organisms mistakenly occupy heterogeneous habitats that are no longer suitable for long-term survival and reproductive success owing to increased predation pressures (Battin, 2004; Ries and Fagan, 2003; Schlaepfer *et al.*, 2002, 2005). In undisturbed forest landscapes, heterogeneous habitats provide improved foraging opportunities and protection from predation. Conversely, anthropogenic disturbances create heterogeneous habitats between forest edges and interiors that contain an increased density of predators. Indirect evidence of edge-related variations in predation pressures manifest as a √– shaped edge response curve in prey species densities (Kokko and Sutherland, 2001).

Numerous theoretical and practical studies indicate the importance of testing and controlling for spatial autocorrelation when determining ecological correlates to spatial patterns (Fortin and Jacquez, 2000; Legendre and Fortin, 1989; Legendre *et al.*, 2002). Spatial autocorrelation is the pattern of relatedness of a set of spatially located data, the extent to which adjoining or neighboring spatial units are more likely to have similar magnitude than by chance alone (Fortin *et al.*, 2002). The main issue in studies of edge effects is that spatial autocorrelation can inflate type I errors in statistical analyses and lead to false-positive results in correlations (Lennon, 2000). Resulting spurious correlations can impact conservation efforts for endangered species (Diniz-Filho *et al.*, 2003). However, few studies of primate conservation and ecology have tested and controlled for spatial autocorrelation.

We provide data on how densities ambient air temperatures, and dendrometrics (tree height and diameter) *Cheirogaleus major* of varied along edge-interior gradients in the Vohibola III Classified Forest in SE Madagascar. Specifically, we sought to answer the following questions: 1) What is the annual activity pattern of *Cheirogaleus major*? 2) Do densities of *Cheirogaleus major* covary with edge proximity? 3) Are there ecological correlates to densities of *Cheirogaleus major*?

METHODS

We collected data in the Vohibola III Classified Forest. Vohibola III is a 2034-ha forest fragment located at 20°43′S and 47°25′E, 200 km SE of the capital of Antananarivo (Fig. 1). Camp Mangatsiaka is located 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 October to March warm, wet season (Lehman, *unpubl. data*). The average annual temperature is 20.2 ± 3.5°C.

Forests are composed predominantly of endemic species of *Tambourissa* (Monimiaceae), *Ephippiandra* (Monimiaceae), and *Ocotea* (Lauraceae) in Vohibola III. There is also a high diversity of bamboos (Poaceae) and epiphytic plants. The matrix is composed entirely of intensive slash-and-burn agriculture. Cultivation involves rice, sugar cane (*Saccharum officinarum* Poaceae), and tobacco (*Nicotiana tabacum* Solanaceae). Though colonizing tree species, such as *Harungana madagascariensis* (Clusiaceae), and woody plants form a secondary thicket in abandoned cultivated areas, there is an abrupt or hard edge between the matrix and forest habitats.

We set up 4 1250-m transects for surveys of *Cheirogaleus major*, ambient temperature, and dendrometrics in Vohibola III. Per Chen (1992) and Malcolm (1994), each transect ran perpendicular from the forest edge into the forest interior. We used numbered flagging tape to mark 10-m increments from the forest edge (0-m mark) into the forest interior (1250 m) for each transect. We used the first tree trunk $>$10 cm dbh on each transect as the edge point for a transect. Each transect was $\geq$1 km and $\leq$3.5 km from the closest transect.

We conducted surveys of *Cheirogaleus major* at 1900–2230 h from May 2003 to May 2005. However, we conducted no survey in January or February owing to site inaccessibility during the annual cyclone season. We surveyed each transect 4 times per mo, for a total of 16 nocturnal surveys each mo in Vohibola III. We rotated starting points for all surveys between

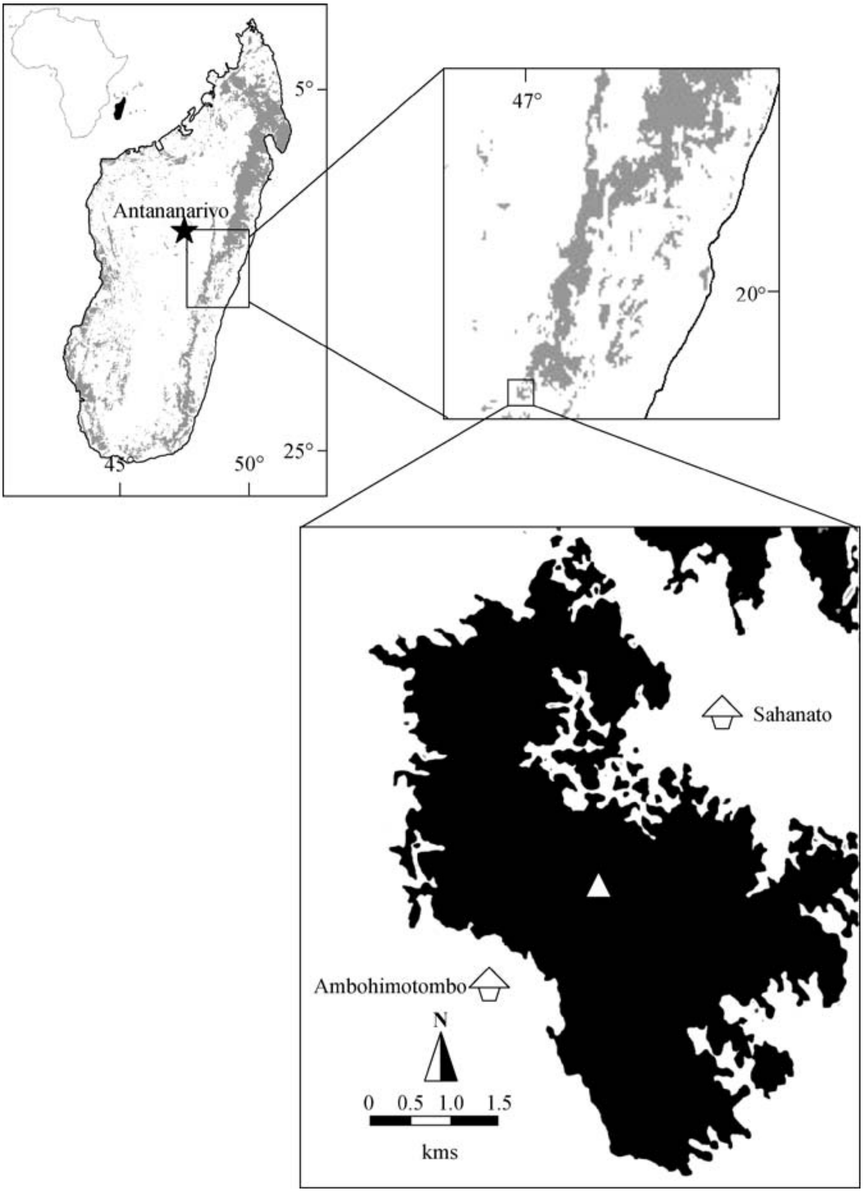

Fig. 1. Location of the Vohibola III Classified Forest. Triangle indicates location of Camp Mangatsiaka.

the edge and 1250-m marks to ensure that there was no bias in the data as a result of increased detection probabilities associated with time periods. We collected the following data whenever we observed *Cheirogaleus major*: date, time, transect number, participants, distance from edge (m), perpendicular sighting distance, height (m) of first individual seen, and method of detection. We estimated density of *Cheirogaleus major* no. of individuals/km^2—by dividing the number of individuals surveyed by the total survey area. We determined densities for 100-m increments, i.e., 0–100 m, 101–200 m, etc., from the forest edge into the interior. We estimated sighting widths for each 100-m increment via the perpendicular distance (m) from the individual to the transect and the histogram inspection technique, with a 50% criterion for falloff distance (Whitesides *et al.*, 1988).

We conducted botanical surveys along both sides of each transect to a depth of 1 m, for a total area sampled of 1 ha. We collected data on height (m), dbh (cm), and distance to forest edge (m) for all trees >10 cm dbh. We collected voucher specimens for each tree identified by local name with the assistance of the local guides. We deposited specimens for scientific identification by botanists at Parc Botanique et Zoologique Tsimbazaza in Antananarivo. We plotted mean tree height and dbh as a function of 100-m increments from the forest edge.

We collected abiotic data on ambient temperatures (°C) via a Kestrel 4000 Weather Tracker (Nielsen-Kellerman, Nelson, PA) at 0930–1430 h along each transect no more than once per day except for days with rain ($N = 394$). One team member collected data holding the Kestrel 4000 at breast height (*ca.* 1.3 m), facing in the cardinal direction of the transect, and waiting until readings had stopped fluctuating. Team members always stayed ≥ 3 m behind the instruments during readings. Per Chen (1995), we collected abiotic data at the following meter marks from the edge into the forest: 0, 5, 10, 15, 30, 45, 60, 90, 120, 150, 180, 210, 240, 270, 300, 360, 420, 480, 540, 600, 720, 840, 960, 1080, 1150, and 1250. We pooled temperature data into 100-m increments for comparison to *Cheirogaleus major* and tree distributions and densities. We measured altitude via the Kestrel 4000 at each 100-m mark along each transect.

We used Kruskal-Wallis tests to determine differences in survey frequencies between transects as well as differences in temporal—month and year—and spatial—edge proximity by transect and perpendicular sighting distances—data on *Cheirogaleus major*. We used a Mann-Whitney *U* test to determine differences in *Cheirogaleus major* edge proximities between transect aspect, i.e., north vs. south. We used linear, quadratic, and cubic regression models (*R*) to determine how densities of *Cheirogaleus major*? temperature, and dendrometrics (dependent variables) varied as a function of distance from forest edge (independent variable). We used polynomial

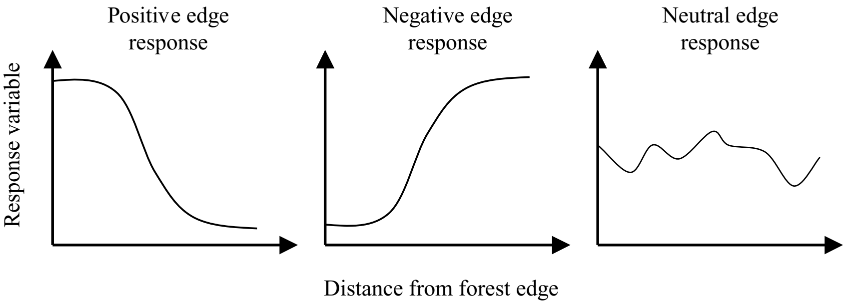

Fig. 2. Three models of how edge effects influence ecological response variables. (Based on Ries *et al.*, 2004.)

regression analyses because there is no reason to assume that edge effects and response variables vary monotonically (Murcia, 1995). If >1 model returned a statistically significant result, then we chose the most parsimonious model provided it did not result in a >5% reduction in the amount of variation in a dependent variable. We analyzed edge-related variations in temperature data via a repeated measures ANOVA. Ries *et al.* (2004) defined 3 classes of ecological edge responses, which we follow here for *Cheirogaleus major* and dendrometrics (Fig. 2). A negative correlation between a response variable and depth into the forest indicates a positive edge response, i.e., higher values in edge habitats. Conversely, a negative edge response occurred when there was a positive relationship between a response variable and depth into the forest, i.e., lower values in edge habitats. If edge proximity did not covary with a response variable, then we classified this pattern as a neutral edge response. We conducted the tests via SPSS 11.5.

We tested for spatial autocorrelation for all variables via a Mantel's test (Z). A Mantel's test is a linear estimate of the relationship between 2 square distance matrices of variables taken at the same sampling locations (Mantel, 1967). The first matrix comprised the Euclidean distances between each depth category, i.e., 100 m vs. 200 m = 100, 100 m vs. 300 m = 200, etc. The second matrix contained the difference between response variables at each depth category, e.g., density of *Cheirogaleus major* at 100 m—value at 200 m. We then normalized each Mantel statistic (Z) into a correlation coefficient (r_m), which corresponds to the intensity of spatial autocorrelation for 2 variables (Fortin and Dale, 2005). Though spatial autocorrelation in only 1 of 2 variables does not affect a test of significance, spatial autocorrelation in both response and environmental variables requires corrections in correlation analyses (Legendre *et al.*, 2002). If only 1 variable exhibited spatial correlation, then we conducted Pearson correlations. If 2 variables

Table I. Transect descriptions and survey frequencies in Vohibola III

		Elevation (m)		Survey frequencies[a]	
Transect	Aspect	Range	Mean ± 1 SD	Temperature	Lemur
I	North	1008–1171	1217.9 ± 18.0	107	46
II	North	1161–1256	1212.9 ± 27.9	97	45
III	South	1065–1164	1108.2 ± 28.0	90	45
IV	South	1008–1171	1126.7 ± 23.3	100	46
Total		1008–1256	1166.3 ± 55.2	394	182

[a] Temperature refers to the number of surveys conducted for this abiotic factor along each transect.

exhibited spatial autocorrelation, then we compared them with a Mantel's test, except that we replaced the Euclidean distance matrix by an ecological variable, i.e., dendrometrics, temperature, and altitude. We included altitude in the correlation models because Johnson *et al.* (2005) suggested it has a stronger influence than edges on diurnal lemur abundance. We assessed statistical significance via a restricted randomization technique with 10,000 iterations (Legendre and Fortin, 1989). We conducted Mantel's tests via the Rundom Project software (Jadwiszczack, 2002), and determined the correlation coefficient r_m via the PopTools add-in for Excel (Hood, 2004). Finally, we constructed a path diagram via the Mantel's correlation values. Path analysis provides a visual means to organize an interpretation of correlational relationships (Petraitis *et al.*, 1996). Path diagrams are interpretative rather than causal. We set the α level $= 0.05$ for all analyses.

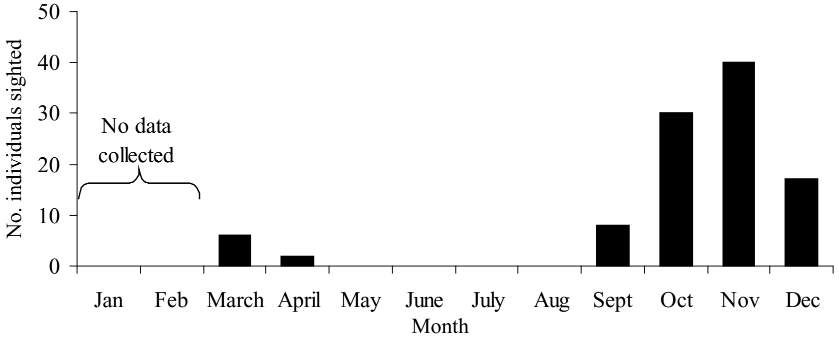

Fig. 3. Frequency distribution of sightings of *Cheirogaleus major* per mo in Vohibola III.

Table II. Linear and polynomial regression models of densities of *Cheirogaleus major?* ambient air temperatures, dendrometrics, and altitude as a function of edge proximity

Variable	Model	R	R^2	F	df	p
Density of *Cheirogaleus major* (no. of individuals/km^2)	Linear	.657	.432	7.62	1, 10	.020
	Quadratic	.742	.551	5.54	2, 9	.027
	Cubic	.759	.577	3.63	3, 8	.064
Ambient temperature (°C)	Linear	.960	.923	117.51	1, 10	.000
	Quadratic	.976	.952	.81	2, 9	.367
	Cubic	.976	.953	10.74	3, 8	.001
Tree height (m)	Linear	.807	.652	18.78	1, 10	.001
	Quadratic	.870	.758	14.09	2, 9	.001
	Cubic	.944	.892	22.25	3, 8	.000
Tree dbh (cm)	Linear	.738	.545	11.99	1, 10	.006
	Quadratic	.761	.579	6.19	2, 9	.020
	Cubic	.842	.708	6.49	3, 8	.015
Altitude (m above sea level)	Linear	.515	.265	3.61	1, 10	.086
	Quadratic	.521	.271	1.68	2, 9	.239
	Cubic	.721	.523	2.89	3, 8	.132

RESULTS

We conducted 182 nocturnal lemur surveys along the 4 transects in Vohibola III (Table I). We observed *Cheirogaleus major* only during March–April and from mid-September through December, with the highest sighting frequency occurring during October–November (Fig. 3). Edge proximity of *Cheirogaleus major* does not vary by mo ($H = 6.28$, df $= 5$, $p = .28$) or by yr ($H = 1.51$, df $= 2, p = .11$). Moreover, *Cheirogaleus major* does not exhibit significant between-transect differences in edge proximity ($H = 2.19$, df $= 3, p = .53$), aspect ($U = 898.5, z = -1.13, p = .25$), or perpendicular sighting distance ($H = 6.75$, df $= 3$, $p = .08$). Thus, we pooled data on edge proximity of *Cheirogaleus major* across time and transects. A quadratic regression model revealed that proximity to the forest edge is a significant determinant of densities of *Cheirogaleus major* explaining 55.1% of the variation in spatial abundance of this species (Table II). Therefore, we classified *Cheirogaleus major* as having a negative edge response in Vohibola III (Fig. 4). There is evidence of spatial autocorrelation in the density response curve of *Cheirogaleus major* ($Z = 62{,}5042.7$, $r_m = 0.425, p = .025$).

Mean ambient air temperatures correlate with distance from the forest edge (Table II; Fig. 5) and displays significant spatial autocorrelation ($Z = -17789.3$, $r_m = -0.860$, $p = .0009$). Edge proximity is also a significant determinant of clinal variations in tree height and dbh. Thus, we classified tree height and dbh as having a negative edge response in

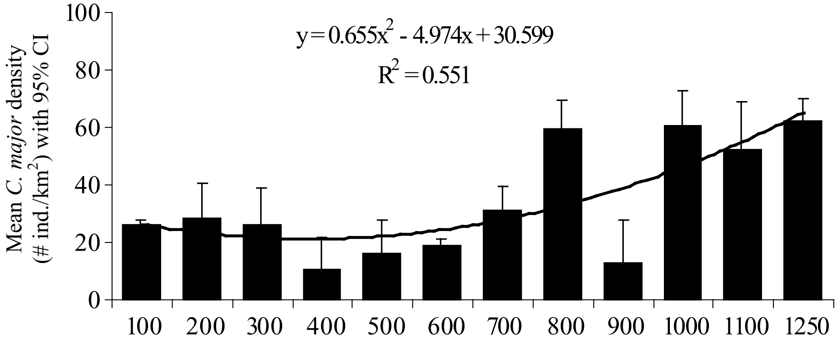

Fig. 4. Edge-related variations in densities of *Cheirogaleus major* in Vohibola III.

Vohibola III. We detected spatial autocorrelation for edge-related variations in tree height ($Z = 52{,}837.1$, $r_m = .569$, $p = .0009$) and dbh ($Z = 47{,}373.9$, $r_m = .496$, $p = .003$). Altitude and edge proximity do not correlate significantly. Moreover, there is no spatial autocorrelation in the altitude data ($Z = -8419.5$, $r_m = .039$, $p = .892$).

Because our study is one of the first to test for spatial autocorrelation in primate ecology, we have also provided the raw Pearson's correlations for edge responses of *Cheirogaleus major* (Table III). However, the 2 correlation coefficients are not directly comparable because Mantel's tests are performed via distance measures and Pearson's tests use the raw data (Legendre and Fortin, 1989). Thus, one should directly compare only significance values (Fortin and Dale, 2005). After we controlled for spatial arrangement of the samples (Fig. 6), densities of *Cheirogaleus major* correlate significantly with tree height and strongly with dbh. Density of *Cheirogaleus major* also correlates negatively with clinal variations in temperature. There is no correlation between density of *Cheirogaleus major* and altitude. Tree height positively correlates with dbh. Temperature correlates negatively with tree height and dbh. Finally, altitude covaries with tree height and dbh, but not with temperature.

DISCUSSION

Our first question pertained to annual activity patterns in *Cheirogaleus major*. We found that *Cheirogaleus major* is inactive May–mid-September in Vohibola III, which matches the pattern reported for conspecifics studied in 1992–1993 in Ranomafana National Park by Wright and Martin (1995), who suggested that the activity pattern related to seasonal

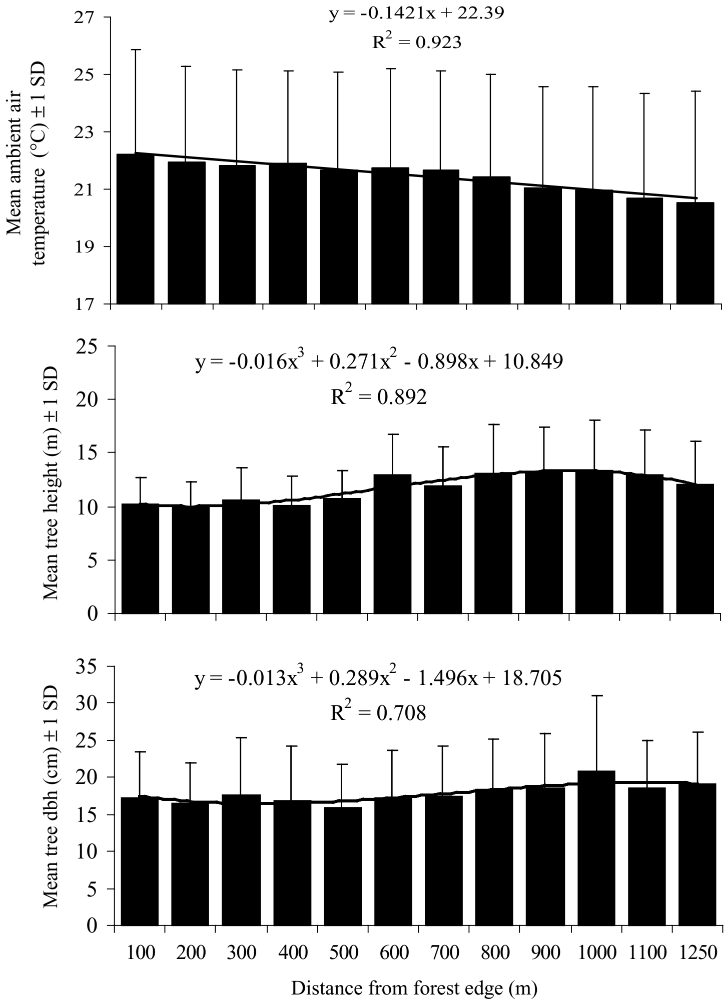

Fig. 5. Edge-related variations in and mean ambient air temperature, mean tree height, and mean tree dbh in Vohibola III.

fruit availability. Specifically, fruit availability tends to be highest from September to December and lowest from April to August in Ranomafana National Park. Though fruiting patterns may be similar between Ranomafana National Park in 1992–1993 and Vohibola III in 2003–2005, research on temporal and geographic variations in fruit availability led us to question the unimodal relationship to activity

Table III. Comparison between Pearson's and Mantel's correlation coefficients for ecological correlates to *Cheirogaleus major* edge responses

	Pearson's		Mantel's	
Variable	r	p	r_m	p
Ambient temperature (°C)	−.656	.021	−.421	.003
Tree height (m)	.504	.095	.197	.01
Tree dbh (cm)	.740	.006	.604	.0009

Note. Owing to statistical differences in how the correlation values are determined, only the significance values are directly comparable.

patterns of *Cheirogaleus major* (Ganzhorn *et al.*, 1999; Hemingway, 1998; Johnson, 2002; Overdorff, 1991). For example, research by Overdorff (1991) and Hemingway (1998) indicates temporal variations in fruit availability in Ranomafana National Park. Overdorff (1991) found that fruit availability, as measured via crown volume, was highest in August–October, with a second peak in February. Few trees produced fruit from April to July. Conversely, in a study conducted only 2 yr later, Hemingway (1998), found that fruiting peaked from September to December for canopy trees and from November and February for understory trees. Moreover, there is no

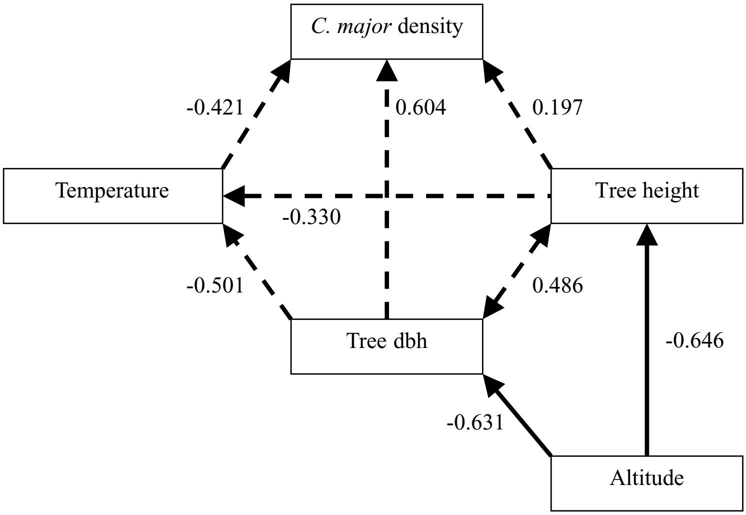

Fig. 6. Path diagram of correlational relationships between abiotic and biotic edge variables. Numeric values represent associated Mantel's and Pearson's correlation coefficients. Solid lines indicate $p \leq .05$; dashed lines indicate $p \leq .01$.

correlation between fruit availability and either temperature or rainfall. Johnson (2002) documented variations in fruit availability for 2 sites only 7 km apart in Andringitra National Park. However, they used different methods to assess phenology. Thus, longitudinal studies of the ecology of *Cheirogaleus major* are needed to determine if annual activity patterns relate directly or indirectly to fruit availability.

Our second question was to determine if densities of *Cheirogaleus major* covaried with edge proximity in Vohibola III. Though *Cheirogaleus major* exhibited a negative edge response, there are density variations along the edge-interior gradient. Specifically, densities of *Cheirogaleus major* are consistent ≤ 300 m of the forest edge (26.0–28.4 individuals/km^2), after which density estimates decrease (10.4–18.9 individuals/km^2) at a depth of 400–600 m. Densities of *Cheirogaleus major* then increase to their highest levels (59.2–62.5 individuals/km^2) at 700–1250 m, except for the low value of 13.0 individuals/km^2 at 900 m from the forest edge. Though we cannot explain the low density value at 900 m, the overall √-shaped edge response curve provides indirect evidence of an ecological trap (Kokko and Sutherland, 2001). Despite a lack of published data on how primate predators respond to edge effects, there is support for predation as a major influence on lemur life histories and behavior (Goodman, 2003; Goodman *et al.*, 1993; Hart, 2000; Wright *et al.*, 1997). For example, Hart (2000) conducted a meta-analysis of biogeographic patterns of primate predation and documented higher predation rates in Madagascar versus the Neotropics, Africa, and Asia. Of the 255 predation events and attacks observed on lemurs, 68% ($N = 190$) were by owls (e.g., *Tyto soumagnei*, *Otus rutilus*, *Asio madagascariensis*, and *Tyto alba*) on small-bodied (<2 kg), nocturnal taxa. Wright and Martin (1995) noted that predators tend to consume *Cheirogaleus major* preferentially during the time period of heaviest body weights for the lemur. Further, Karpanty (2003) observed that diurnal lemurs are aware of and able to distinguish between different types of aerial predators. The ecological trap hypothesis could be tested by comparisons among edge, transitional, and interior habitats of 1) the frequency and abundance of *Cheirogaleus major* remains in avian nests and owl scat (Goodman *et al.*, 1993; Karpanty, 2003), 2) frequencies of responses of *Cheirogaleus major* to alarm calls made by conspecifics (Fichtel and Kappeler, 2002; Karpanty, 2003), and 3) population dynamics *Cheirogaleus major* from capture-release data (Wolf and Batzli, 2002). Obviously, the second method would require data on whether or not *Cheirogaleus major* actually gives alarm calls after detecting potential animal predators.

Our third question focused on determining ecological correlates to edge responses of *Cheirogaleus major*. Though densities of *Cheirogaleus major* covary significantly with temperature and tree height, the correlation values are low, particularly for the effects of tree height on density ($r = .197$). Moreover, ambient air temperature covaries with tree height and dbh, likely because of larger trees blocking more sunlight than smaller trees do. Thus, we suggest that *Cheirogaleus major* are responding only indirectly to clinal variations in temperature. Conversely, tree dbh correlates strongly with edge-related variations in the density of *Cheirogaleus major*, even after controlling for spatial autocorrelation. Tree diameter tends to covary with fruit abundance in Madagascar (Balko and Underwood, 2005; Ganzhorn, 1995). If *Cheirogaleus major* is highly frugivorous (Wright and Martin, 1995) and dbh/fruit production are negatively influenced by edge proximity, then clinal variations in fruit production can explain the spatial patterns we observed for the lemur in Vohibola III. Despite the highly significant correlation between densities of *Cheirogaleus major* and tree dbh, lemur ecologists have documented other covariates to fruit production in eastern humid forests. Specifically, Balko and Underwood (2005) documented that fruit production covaries with dbh and to an even greater degree, crown volume, in Ranomafana National Park. However, researchers typically estimate crown volume via indirect measurements of crown dimensions and shape. Further, fruiting patterns vary seasonally and geographically in the eastern humid forests of Madagascar (Ganzhorn *et al.*, 1999; Johnson, 2002; 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 (2002) noted different temporal patterns of fruit production between Andringitra and Ranomafana National Parks, which are only 115 km apart in SE Madagascar. Specifically, fruit production was highest from December to May in Andringitra and July–December in Ranomafana National Park. Our dendrometric data are for all trees rather than just for food trees. It is highly likely that the data include tree species that do not represent an important fruit resource for *Cheirogaleus major*. Thus, one should view correlates between edge responses of *Cheirogaleus major* and tree dbh as an indirect measure of fruit abundance with caution.

Cheirogaleus major also feeds regularly on nectar from the flowers of the liana *Strongylodon craveniae* (Leguminosae) during November and December (Nilsson *et al.*, 1993; Wright and Martin, 1995). Though there are few data on edge effects on liana abundance, lianas tend to be larger in diameter and more abundant on large trees (Johnson and Overdorff, 1999; Nilsson *et al.*, 1993; Perez-Salicrup *et al.*, 2001; Zurring *et al.*, 1993). Given the clinal variations in tree dbh we documented in Vohibola III, there may be concomitant spatial variations in the abundance of lianas. Therefore, edge-related variations in densities of *Cheirogaleus major* may also relate to spatial patterns for *Strongylodon craveniae* (Leguminosae).

Despite methodological issues with determining the relationship between dbh and food production, our data on edge responses of *Cheirogaleus major* have important implications for other frugivorous lemurs. For example, the black-and-white ruffed lemur (*Varecia variegata variegata*) is highly frugivorous (Balko and Underwood, 2005; Britt, 2000; Ratsimbazafy, 2002), and is listed by the IUCN as endangered (IUCN, 2005). Moreover, recent surveys have revealed a dramatic decline in the distribution of *Varecia variegata variegata* in SE Madagascar (Lehman *et al.*, 2006c), including its absence in Vohibola III. *Varecia variegata variegata* tend to select fruit from trees with large diameters and crowns (Balko and Underwood, 2005; Britt, 2000), though changes in forest structure after hurricanes can alter the pattern (Ratsimbazafy, 2002). If large fruit trees are negatively influenced by edge proximity, then *Varecia variegata variegata* should be particularly susceptible to edge effects. Therefore, researchers should prioritize studies of how *Varecia variegata variegata* respond to edge effects.

We found that spatial autocorrelation was a consistent issue for each of the ecological data sets, which has important implications for primate ecology and conservation biology. Though some researchers have suggested that all regression and correlation statistics without spatial controls are flawed (Lennon, 2000), recent theoretical and practical studies indicate that spatial autocorrelation does not always generate bias (Diniz-Filho *et al.*, 2003; Fortin and Dale, 2005; Legendre *et al.*, 2002). If spatial autocorrelation exists in multiple variables, then failure to control for the effect can result in the overestimation of regression models (Legendre and Fortin, 1989). Spatial autocorrelation is also an important factor to consider in studies of macroscale specific diversity (Willis and Whittaker, 2002). For example, Diniz-Filho *et al.* (2003) found that spatial autocorrelation can exist $\leq$ 1600 km for bird species richness in Europe, north Africa, and the Middle East. They noted that controlling for spatial autocorrelation deemphasized long-distance effects, such as latitude, in favor of variables, such as elevation, acting at smaller geographical scales. Therefore, it is important that future studies of primate ecology and conservation biology determine the influence of spatial autocorrelation on data, particularly if the researchers make suggestions regarding conservation priorities for endangered species.

Cheirogaleus major exhibits a negative edge response in Vohibola III. This edge response correlates with clinal variations in tree diameter instead of with tree height, temperature, or altitude in Vohibola III. Ultimately, correlates between densities of *Cheirogaleus major* and dbh may reflect spatial patterns of food abundance. Increased sample sizes for surveys and data on food abundance will provide a greater understanding of how *Cheirogaleus major* responds to edge effects. For example, if there are interannual variations in fruit production, then we would predict concomitant variations in edge responses of *Cheirogaleus major*. Ongoing surveys should provide us with sufficient data to describe edge responses for other frugivorous lemurs in Vohibola III: *Propithecus diadema edwardsi* and *Eulemur fulvus rufus*. Data are needed on how forests and lemurs are influenced by edge effects in other biogeographic regions in Madagascar. Future studies of primate ecology and conservation biology should incorporate tests and controls for spatial autocorrelation.

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