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Spatial Variations in *Eulemur fulvus rufus* and *Lepilemur mustelinus* Densities in Madagascar

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Key Words

Forest fragmentation · Edge habitats · *Lepilemur mustelinus* · *Eulemur fulvus rufus* · Density · Seed dispersal · Frugivory · Folivory

Abstract

I present data on variations in *Eulemur fulvus rufus* and *Lepilemur mustelinus* densities as well as tree characteristics (height, diameter and stem frequency) between edge and interior forest habitats in southeastern Madagascar. Line transect surveys were conducted from June 2003 to November 2005 in edge and interior forest habitats in the Vohibola III Classified Forest. Although *E. f. rufus* densities were significantly lower in edge habitats than in interior habitats, density estimates for *L. mustelinus* did not differ significantly between habitats. Trees in edge habitats were significantly shorter, had smaller diameters and had lower stem frequencies (for those >25 cm in diameter) than trees in interior habitats. Spatial characteristics of food abundance and quality may explain lemur density patterns in Vohibola III. Low *E. f. rufus* densities may reduce seed dispersal in edge habitats, which has important consequences for the long-term viability of forest ecosystems in Madagascar.

Introduction

Anthropogenic disturbances are causing forests to become increasingly fragmented in many tropical regions of the world. One of the main consequences of forest fragmentation is an increase in the amount of edge habitats [Laurance and Yensen, 1991]. Edge habitats occur at the boundary between two different habitat types, such as where grasslands border on forests. Edge habitats have transitional abiotic (temperature, humidity, light levels, wind speed) and biotic characteristics that can benefit certain species but exclude others over time [Ries and Sisk, 2004]. Murcia [1995]

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noted that these spatial and temporal variations in habitat characteristics can then have secondary effects on pollination and seed dispersal. For example, increased wind speed near forest edges causes blow-down damage to large fruit trees [Laurance and Yensen, 1991]. Destruction of large fruit trees near forest edges results in reduced densities of frugivores in these habitats, which ultimately has a negative effect on forest dynamics if the frugivores are also important pollinators and seed dispersers [Restrepo et al., 1999]. However, some tropical mammals prefer forest edges due to higher leaf quality and insect abundance in these habitats [Ries et al., 2004]. Ganzhorn [1995] documented that low-intensity logging increased light levels in dry forests in western Madagascar, which resulted in a higher protein concentration in leaves. Thus, some folivorous primates may prefer to forage for leaves in edge habitats. However, there are few data on spatial variations in primate abundance between edge and interior habitats.

Primate responses to forest edges are particularly relevant to lemurs, which are among the most threatened primate taxa in the world due to extremely high levels of forest loss and fragmentation in Madagascar [Mittermeier et al., 1994; Ganzhorn et al., 2001; Lehman, 2006]. In fact, recent studies by Ganzhorn et al. [2003] documented a positive correlation between fragment size and lemur species diversity in southeastern Madagascar. Most lemurs are either unwilling or unable to cross grassland and agricultural fields between forest fragments [Lehman, 2006]. However, many lemurs persist in degraded and edge habitats [Ganzhorn, 1994, 1995; Irwin et al., 2005; Lehman et al., 2006a]. For example, of the 6 lemur taxa studied to date for their responses to forest edges in eastern humid forests *(Avahi laniger*, *Cheirogaleus major*, *Eulemur rubriventer*, *Hapalemur griseus griseus*, *Microcebus rufus* and *Propithecus edwardsi),* only *C. major* had reduced densities in edge habitats [Lehman et al., in press a]. The other 5 lemur taxa existed at either higher densities in edge habitats or they did not display any spatial variations in densities [Lehman et al., 2006a]. Little is known about how other sympatric lemur taxa, such as *Eulemur fulvus* and *Lepilemur* sp., respond to forest edges.

E. f. rufus is a medium-sized (2.18–2.25 kg) lemur that tends to be found in primary and well-established secondary humid forests in southeastern Madagascar [Overdorff, 1993; Smith and Jungers, 1997]. This diurnal lemur lives in multi-male, multi-female groups with an average group size of 9 individuals in Ranomafana National Park [Overdorff et al., 1999]. Density estimates for *E. f. rufus* (3.8–22.7 individuals/km^2) vary widely throughout southeastern Madagascar [Overdorff, 1991; Irwin et al., 2005; Lehman et al., 2005]. The annual diet of this lemur is dominated by fruit and supplemented by seasonal exploitation of leaves and flowers [Overdorff, 1991]. The taxonomic status and biogeography of nocturnal *Lepilemur* sp. is the subject of considerable debate [Groves, 2001; Ravaoarimanana et al., 2001; Goodman and Ganzhorn, 2003]. Following recent cytogenetic studies, the *Lepilemur* taxa in the region of my study site may represent a new, undescribed species [Andriaholinirina et al., 2005]. Until such time as this debate is resolved, the *Lepilemur* taxon in this region is listed as *L. mustelinus* [Goodman and Ganzhorn, 2003]. This species of sportive lemur weighs approximately 0.777 kg [Smith and Jungers, 1997] and is found in primary and secondary forests in southeastern Madagascar. *L. mustelinus* is a solitary forager, although 2–4 individuals will sleep together during the day [Lehman, pers. observation]. *L. mustelinus* exists at densities of 9–13 individuals/km^2 in the Anamalazoatra and Vohibola III Special Reserves [Ganzhorn, 1988;

Lehman et al., 2005]. Preliminary data on the feeding ecology of *L. mustelinus* indicate that it prefers leaves and supplements its diet with fruit and flowers [Ganzhorn, 1988]. It is important to note that *L. mustelinus* has a very long cecum [Chivers, 1994], which likely serves as a gastrointestinal adaptation for carbohydrate fermentation [Lambert, 1998].

I generated predictions on how *E. f. rufus* and *L. mustelinus* should respond to edge habitats based on tree characteristics and species-specific dietary patterns [Sussman, 1987]. Fruiting trees tend to occur at low densities and produce few fruit crops in eastern Madagascar [Ganzhorn, 1995]. Moreover, fruit crops tend to be lost due to increased wind turbulence near the forest edge, particularly during the annual cyclone season from January to March [Balko and Underwood, 2005]. For example, cyclonic winds resulted in the total devastation of most fruit patches in Manombo Special Reserve [Ratsimbazafy, 2002; Wright et al., 2005]. Anthropogenic disturbances and cyclone damage to fruit trees can strongly influence the abundance and dispersal of frugivorous lemurs [Balko and Underwood, 2005]. If edge effects negatively influence the distribution and density of fruit trees, then these patch dynamics may be of particular consequence for frugivorous *E. f. rufus*. Therefore, I predicted that *E. f. rufus* should exist at lower densities in edge habitats than in interior habitats. Although changes in fruit availability should also influence *L. mustelinus*, the predominantly folivorous diet of this lemur should mitigate edge influences on spatial patterns of density. Specifically, folivores do not face the same challenges of resource acquisition because of the relatively high abundance and availability of leaves compared to fruits in eastern humid forests [Overdorff, 1993; Powzyk and Mowry, 2003]. Thus, I predicted that there should be no spatial variations in densities for *L. mustelinus* between edge and interior habitats.

Methods

Data were collected from June 1, 2003, to November 22, 2005, at Camp Mangatsiaka in the Vohibola III Classified Forest. No data were collected in January or February due to site inaccessibility during the annual cyclone season. Vohibola III is a 2,034-ha forest fragment located at 20°43′ S and 47°25′ E, 200 km southeast of the capital of Antananarivo. Camp Mangatsiaka is located at 20°41′32″ S, 47°26′15″ E (1,180 m altitude) in the central section of Vohibola III [Lehman et al., 2006a]. Rainfall amounts average 2,478 mm/year, and the heaviest rains tend to come during the warm, wet season from December to March [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). Although 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.

Four 500-meter interior and four 500-meter edge transects were used for lemur and tree surveys in Vohibola III (table 1). Following Chen et al. [1992], each transect ran perpendicular from the forest edge into the forest interior. Numbered flagging tape was used to mark 10-meter increments along each transect. The first tree trunk >10 cm DBH (diameter at breast height) encountered on each transect was used as the edge point. It is important to note that these edge points were always within 0.5 m of the 'hard' edge between the forest and matrix. In other

Table 1. Transect descriptions and survey frequencies in Vohibola III

Transect	Habitat	Survey frequencies	
		diurnal	nocturnal
1	edge	152	58
2	interior	152	58
3	edge	146	56
4	interior	146	56
5	edge	138	56
6	interior	138	56
7	edge	142	58
8	interior	142	58
Total		1,156	456

words, the start of each transect was not separated from the edge by a large expanse of secondary vegetation with a DBH <10 cm. Interior transects were set up at the same orientation and 250 m from the terminus of edge transects. Thus, interior transects started 750 m from the forest edge, which exceeds penetration distances for all abiotic (temperature, light, humidity and wind) and biotic (tree dendrometrics and densities) edge effects measured in Vohibola III [Lehman, unpubl. data] as well as other forest sites in Madagascar [Lehtinen et al., 2003]. Therefore, survey data for interior transects were extended far enough into forest interior to be free of abiotic and biotic edge effects [Murcia, 1995]. It is important to note that previous studies revealed no significant topographic effects on edge-related variations in abiotic and biotic factors in Vohibola III [Lehman et al., in press a]. Moreover, the maximum elevation of 1,311 m in Vohibola III is well below the maximum elevation reported by Goodman and Ganzhorn [2004] for *E. f. rufus* (1,670 m) and *L. mustelinus* (1,990 m).

Diurnal lemur surveys were conducted along transects by 1–3 team members walking slowly (0.5–1.0 km/h) during 7.00–11.00 h and 14.00–17.00 h. Nocturnal surveys were conducted by 1–2 team members along transects from 19.00 to 22.30 h. Starting points for all surveys were rotated to ensure that the data were not biased due to increased detection probabilities associated with time. The following data were collected whenever lemurs were seen: date, time, transect number, participants, distance along trail from first animal seen/middle of group, species/subspecies, group composition and size, perpendicular sighting distance, height (m) of first animal seen, group spread and method of detection.

Botanical surveys were conducted along both sides of each transect to a depth of 1 m, for a total area sampled of 0.8 ha. Data were collected on height (m), DBH (cm) and distance to forest edge (m) for all trees >10 cm DBH. The 10-cm DBH threshold is a standard limit used by primatologists throughout southeastern Madagascar and thus facilitates direct comparisons between sites. Voucher specimens were collected for each tree identified by local name with the assistance of the local guides. Specimens were deposited for scientific identification by botanists at the Parc Botanique et Zoologique Tsimbazaza in Antananarivo.

Lemur densities (number of individuals/km^2) were obtained by dividing the number of individuals surveyed by the total survey area in each habitat [Whitesides et al., 1988]. Species-specific sighting widths for each transect were estimated using the perpendicular distance (m) from the individual or center of the group to the transect and the histogram inspection technique, with a 50% criterion for falloff distance [Whitesides et al., 1988]. Variances were computed by using each transect sample separately.

Table 2. Differences in perpendicular sighting distances and density estimates for *E. f. rufus* and *L. mustelinus* between edge and interior habitats

Lemur taxa	Individuals		Mean perpendicular distance ± 1 SD, m		p	Density ± variance, individuals/km^2		p	Edge response
	edge	interior	edge	interior		edge	interior		
E. f. rufus	30	87	6.8 ± 5.9	6.5 ± 4.1	>0.10	6.0 ± 1.3	12.4 ± 0.8	<0.001	negative
L. mustelinus	22	25	5.2 ± 2.7	5.4 ± 3.0	>0.10	9.8 ± 2.4	12.3 ± 2.1	>0.10	neutral

Pearson χ^2 tests were used to determine differences in diurnal and nocturnal survey frequencies between transects as well as differences in tree stem numbers between habitats. I used Kruskal-Wallis tests to determine seasonal differences in density estimates for *E. f. rufus* and *L. mustelinus.* Seasons were defined as follows: rainy season from December to April, cool dry season from May to August and dry season from September to November [Grassi, 2002; Lehman, in press]. A two-sample, structured randomization test with 10,000 iterations was used to determine habitat differences in lemur perpendicular sighting distances, lemur densities and dendrometrics. This test was used because it is responsive to edge-related data sets and requires no assumptions regarding the underlying distribution of the data [Fortin and Dale, 2005]. Only significance values are reported because randomization tests do not produce a statistical test value. Randomization tests were computed using the Pop Tools add-in for Microsoft Excel [Hood, 2004]. The α level was set at 0.05 for all analyses. Following Ries et al. [2004], I used 3 classes of edge responses for lemurs and tree characteristics. Taxa with significantly higher density estimates or characteristics in edge habitats exhibited a positive edge response. Taxa with significantly lower density estimates or characteristics in edge habitats exhibited a negative edge response. A neutral edge response occurred when there were no differences in lemur density or tree characteristics between interior and edge habitats.

Results

A total of 1,156 diurnal lemur surveys and 456 nocturnal lemur surveys were conducted along the 8 transects in Vohibola III (table 1). There were no significant differences in the distribution of either diurnal surveys ($\chi^2 = 0.73$, d.f. = 7, $p > 0.10$) or nocturnal surveys ($\chi^2 = 0.07$, d.f. = 7, $p > 0.10$) across the 8 transects. There were no seasonal effects on density estimates for *E. f. rufus* (H = 5.18, d.f. = 2, p = 0.28) or *L. mustelinus* (H = 4.30, d.f. = 2, p = 0.15). Moreover, there were also no variations in perpendicular sighting distances for either *E. f. rufus* or *L. mustelinus* between edge and interior habitats (table 2). Thus, any spatial variations in lemur density estimates were not an artifact of seasonal variations in activity levels, survey effort or differential detection probabilities between habitats. *E. f. rufus* had significantly lower densities in edge habitats than in interior habitats. Density estimates for *L. mustelinus* did not differ significantly between habitats. Therefore, *E. f. rufus* was classified as having a negative edge response and *L. mustelinus* was classified as having a neutral edge response.

Tree data for each habitat type are in table 3. Trees were significantly shorter in edge habitats than in interior habitats. Similarly, mean DBH was significantly small-

Table 3. Comparisons of tree characteristics between edge and interior habitats

Tree characteristic	Edge	Interior	p value	Edge response
Mean height ± 1 SD, m	10.34 ± 2.7	12.76 ± 4.3	<0.0001	negative
Mean DBH ± 1 SD, cm	16.89 ± 6.7	19.04 ± 7.6	<0.0001	negative
Stems >10 cm DBH	517	542	>0.10	neutral
Stems >25 cm DBH	119	207	<0.001	negative

er in edge habitats than in interior habitats. Although there were no significant differences in the total number of tree stems between habitats ($\chi^2 = 0.25$, d.f. = 1, $p > 0.10$), there were significantly fewer trees with a DBH >25 cm in edge habitats ($\chi^2 = 11.5$, d.f. = 1, $p < 0.001$). Thus, trees exhibited an overall negative edge response in Vohibola III.

Discussion

I confirmed my first prediction that *E. f. rufus* would exist at lower densities in edge habitats than in interior habitats. These spatial variations in the abundance of *E. f. rufus* are likely a result of the combined effects of a frugivorous diet and tree dendrometrics. During periods of fruit scarcity, *E. f. rufus* feed on fruit from large trees of rare plant species in Ranomafana National Park [Overdorff, 1993], which is only 40 km south of Vohibola III. *E. f. rufus* also forage for fruit over wider areas of forest than sympatric *E. rubriventer.* Tree diameter tends to covary with fruit abundance in Madagascar [Ganzhorn, 1995; Balko and Underwood, 2005], and tree DBH is significantly smaller in edge habitats in Vohibola III. There are also fewer large trees in edge than interior habitats. If tree diameter and fruit production are negatively influenced by edge proximity, then spatial variations in fruit production explain some of the density patterns observed for *E. f. rufus* in Vohibola III. Reduced densities of *E. f. rufus* in edge habitats may have important secondary effects on forest processes. Despite *E. f. rufus* being poor pollinators due to their destructive flower feeding [Overdorff, 1992], they are thought to be important seed dispersers of fruit trees in southeastern Madagascar [Dew and Wright, 1998]. Therefore, the negative edge response by *E. f. rufus* may ultimately be detrimental to forest processes in southeastern Madagascar.

It is important to note that my tree data are for all species rather than just for food trees exploited by *E. f. rufus* in Vohibola III. Although *E. f. rufus* feed on 104 plant species [Overdorff, 1993], it is highly likely that my dendrometric data include species that do not represent an important food resource for *E. f. rufus*. Moreover, the diet of *E. f. rufus* may vary between edge and interior habitats. Studies of lemur feeding ecology indicate that conspecifics can exhibit considerable dietary differences between habitats [Lehman and Mayor, 2004; Balko and Underwood, 2005]. Any presumed relationships between *E. f. rufus* edge responses and tree characteristics, as an indirect measure of fruit abundance, should be viewed with caution.

My second prediction was also confirmed in that *L. mustelinus* exhibited a neutral edge response in Vohibola III. This neutral edge response is likely due to the fact that the abundance of leaves is not influenced by edge effects [Norconk and Grafton, 2003]. Despite the lack of statistical difference in *L. mustelinus* densities between habitats, there was a tendency for this species to be more abundant in interior than edge habitats (table 2). Edge-related variations in fruit abundance are possible covariates to the distribution of *L. mustelinus* in Vohibola III. Thus, an interesting question that cannot be answered at this time is if *L. mustelinus* will exhibit a negative edge response, similar to that seen in the highly frugivorous *E. f. rufus*, during the time period of maximum fruit availability (approx. from January to May). Moreover, the broad habitat characteristics used here may mask fine-grained responses of folivorous lemurs to spatial variations in leaf quality (protein and energy). For example, *Avahi laniger* is a small-bodied (0.60–1.30 kg), highly folivorous lemur that is sympatric with *L. mustelinus* throughout much of southeastern Madagascar [Faulkner and Lehman, 2006], except for Kalambatritra Special Reserve, in which no *A. laniger* have been seen but *Lepilemur* sp. are abundant [Irwin et al., 2001]. Despite *A. laniger* exhibiting a neutral edge response using broad edge versus interior habitats [Lehman et al., 2006a], detailed spatial data revealed that this species is most abundant within 100 m of the forest edge [Lehman et al., 2006b]. Edge-related variations in *A. laniger* densities are likely a result of higher protein levels in leaves near forest edges [Ganzhorn, 1995] as well as small body size and the simple monogastric stomach of this lemur [Faulkner and Lehman, 2006]. Spatial variations in protein levels should also be relevant to *L. mustelinus.* The cecocolic fermentation used by *Lepilemur* sp. precludes the use of protein from fermentative gut microbes [Lambert, 1998]. This lemur also lacks large body size, which is one of the main morphological adaptations associated with folivory [Chivers and Hladik, 1980]. Specifically, it has been hypothesized that a highly folivorous diet can only be energetically sustained by a primate weighing more than 0.700 kg [Kay, 1984]. Therefore, the neutral edge response of *L. mustelinus* needs to be verified at more fine-grained spatial scales.

The negative edge response exhibited by *E. f. rufus* and slightly lower density of *L. mustelinus* in edge habitats may also reflect past hunting practices by local people. Although hunting by local people has ceased since they decided in approximately 1999 to designate Vohibola III as a protected area, lemurs are hunted and *E. f. rufus* is a favorite prey item in the adjacent Fandriana-Marolambo Forest Corridor [Lehman et al., 2006c; Lehman et al., in press b]. In this corridor, hunting is typically done with blow guns, sling shots and snare traps. Moreover, lemur snare traps were found to be in close proximity to forest edges in the northern part of the corridor [Lehman and Wright, 2000]. If local people are actively hunting lemurs with snare traps in Vohibola III, then the indiscriminant capture of all lemurs in these traps should have also resulted in significantly lower density estimates for *L. mustelinus* in edge habitats. However, density estimates were only reduced for *E. f. rufus* in edge habitats. Moreover, previous research found that *Propithecus edwardsi*, which is heavily hunted by people in southeastern Madagascar, actually exists at higher densities in edge habitats in Vohibola III [Lehman et al., 2006b]. Thus, spatial patterns in lemur densities may represent a lag effect of past hunting/trapping pressures in edge habitats.

In summary, frugivorous *E. f. rufus* avoided edges due presumably to reduced fruit abundance in this habitat, which may have negative effects on seed dispersal of fruit trees. Although tree height and diameter were reduced in edge habitats, folivorous *L. mustelinus* exhibited little spatial variation in density estimates. Lack of an edge response in *L. mustelinus* was likely a result of similar levels of leaf abundance in edge and interior habitats. Increased sample sizes for surveys as well as data on food abundance and quality will provide a more detailed understanding of how *E. f. rufus* and *L. mustelinus* respond to forest edges. Ongoing surveys will also enable me to determine fine-grained variations in edge responses for *E. f. rufus* and *L. mustelinus* in Vohibola III. Continued research on lemur and plant responses to edge habitats will improve our understanding of the conservation biology of forest ecosystems in Madagascar.

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