

BRIEF REPORT

Lemur Responses to Edge Effects in the Vohibola III Classified Forest, Madagascar

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Forest edges are dynamic zones characterized by the penetration (to varying depths and intensities) of conditions from the surrounding environment (matrix) into the forest interior. Although edge effects influence many tropical organisms, they have not been studied directly in primates. Edge effects are particularly relevant to lemurs because of the highly fragmented forest landscapes found in Madagascar. In this study, data are presented regarding how the densities of six lemur species (*Avahi laniger*, *Cheirogaleus major*, *Eulemur rubriventer*, *Hapalemur griseus griseus*, *Microcebus rufus*, and *Propithecus diadema edwardsi*) varied between six 500-m interior transects and six 500-m edge transects in the Vohibola III Classified Forest in SE Madagascar. Diurnal ($n = 433$) and nocturnal ($n = 128$) lemur surveys were conducted during June–October 2003 and May–November 2004. *A. laniger*, *E. rubriventer*, and *H. g. griseus* exhibited a neutral edge response (no differences in densities between habitats). *M. rufus* and *P. d. edwardsi* had a positive edge response (higher densities in edge habitats), which may be related to edge-related variations in food abundance and quality. Positive edge responses by *M. rufus* and *P. d. edwardsi* may ultimately be detrimental due to edge-related anthropogenic factors (e.g., hunting by local people). The negative edge response exhibited by *C. major* (lower densities in edge habitats) may result from heightened ambient temperatures that inhibit torpor in edge habitats. *Am. J. Primatol.* 68:293–299, 2006.

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INTRODUCTION

Edges are dynamic zones characterized by the penetration (to varying depths and intensities) of conditions from the surrounding environment (matrix) into the forest interior [Malcolm, 1997]. Changes in population dynamics as a consequence of edge effects can be defined as indirect biological effects [Murcia,

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1995]. Indirect biological effects represent one of the least studied aspects of primate ecology and conservation biology. Although edge effects have been invoked as a significant determinant of primate distributions in previous studies [Mbona & Meikle, 2004; Tweheyo et al., 2004], those studies used only subjective measures of edge penetration distances. As a result, the survey data may not have extended far enough into forest interiors to be free of abiotic and biotic edge effects [Murcia, 1995].

Primate responses to edge effects may be particularly relevant for lemurs. Lemurs are one of the most threatened primate taxa in the world, due in part to the loss of 80–90% of forest habitats in Madagascar [Du Puy & Moat, 1998]. Although the remaining forest is highly fragmented and may be prone to extreme edge effects, few data are available regarding how edge effects influence lemur biogeography. Ries et al. [2004] defined three classes of ecological edge responses, which we follow here. A species that has a higher density in edge habitats exhibits a positive edge response. A negative edge response occurs when a species has a higher density in interior habitats. Species that exhibit no response to edges have a neutral edge response.

In this paper we present data regarding how densities of *Avahi laniger*, *Cheirogaleus major*, *Eulemur rubriventer*, *Hapalemur griseus griseus*, *Microcebus rufus*, and *Propithecus diadema edwardsi* vary between interior and edge habitats in the Vohibola III Classified Forest in southeast Madagascar.

MATERIALS AND METHODS

Data were collected from 1 June to 29 October 2003, and 28 May to 12 November 2004 at Camp Mangatsiaka in the Vohibola III Classified Forest. These data were used specifically to avoid conflating seasonal variations in ranging patterns with edge effects [Fortin et al., 1996]. Moreover, this time period is associated with food resource scarcity for lemurs in southeast Madagascar [Overdorff, 1993]. Thus, edge effects should be particularly relevant for the ranging patterns of lemurs. Vohibola III is a 2,034 ha forest fragment located at 20°43' S and 47°25' E, 40 km north of Ranomafana National Park. Camp Mangatsiaka is located at 20°41' 32' S, 47°26' 15' E (1,180 m altitude) in the central section of Vohibola III. Rainfall amounts average 2,650 mm per year, and the heaviest rains tend to come during the October–March warm, wet season in southeast Madagascar [Wright, 1999]. The average annual temperature is 21°C in humid forests in southeast Madagascar [Overdorff, 1993].

The forests in Vohibola III are composed predominantly of endemic species of *Tambourissa* (Monimiaceae), *Ehippiandra* (Monimiaceae), and *Ocotea* (Lauraceae). There is also a high diversity of bamboos (Poaceae) and epiphytic plants [Lowry et al., 1997]. 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 the forest habitats.

Six 500-m interior and six 500-m edge transects were set up for lemur surveys in Vohibola III. Following Chen et al. [1992], each of the transects ran perpendicular from the forest edge into the forest interior. The first tree trunk >5 cm diameter at breast height (dbh) encountered on each edge transect was used as the edge point. Interior transects were set up at the same orientation and 250 m from the terminus of the 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, unpublished data]. Numbered flagging tape was used to mark 10-m increments along each transect. The transects were walked slowly (0.5–1.0 km/hr) by one to three team members during 0700–1100 hr and 1400–1700 hr ($n = 433$). Surveys for nocturnal lemurs were conducted from 1900 to 2230 hr ($n = 128$). The starting points for all surveys were rotated to ensure that the data were not biased due to increased detection probabilities associated with time of day/night. The following data were collected whenever lemurs were seen: date, time, transect number, participants, distance along the trail from the first animal seen and the middle of the group, species/subspecies, group composition and size, perpendicular sighting distance, height (m) of the first animal seen, group spread, and method of detection used.

Mann-Whitney U -tests were used to determine whether there were any differences in detection distances between habitats (i.e., edge vs. interior) for each species. We determined lemur densities (number of individuals/km²) 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 (solitary taxa) or center of the group (with adjustment for group spread) to the transect and the histogram inspection technique, with a 50% criterion for falloff distance [Whitesides et al., 1988]. Variances for densities were obtained by treating each transect survey as a separate replicate. A two-sample randomization test with 1,000 iterations was used to determine whether there were significant variations in density estimates between habitats for each species. This test was used because it is responsive to edge-related data sets, is applicable to small sample sizes, and requires no assumptions regarding the underlying distribution of the data [e.g., Fortin & Jacquez, 2000; Lehtinen et al., 2003; Manly, 1997]. Only significance values (P) are reported, because randomization tests do not produce a statistical test value. Randomization tests were computed using the PopTools add-in for Microsoft Excel [Hood, 2004]. The alpha level was set at 0.05 for all analyses.

RESULTS

There were no significant differences in perpendicular detection distances between edge and interior transects for *A. laniger* ($U = 594.0$, $Z = -1.16$, $P = 0.24$), *C. major* ($U = 260.5$, $Z = -1.20$, $P = 0.22$), *E. rubriventer* ($U = 708.0$, $Z = -0.09$, $P = 0.92$), *H. g. griseus* ($U = 82.0$, $Z = -1.81$, $P = 0.07$), *M. rufus* ($U = 318.5$, $Z = -1.76$, $P = 0.07$), or *P. d. edwardsi* ($U = 2.0$, $Z = -1.78$, $P = 0.10$). Thus, our data are not an artifact of differential detection probabilities between habitats. The density of *A. laniger* was 26.0 ± 11.7 ind./km² ($n = 67$) for the interior transects, and 18.7 ± 9.5 ind./km² ($n = 55$) for the edge transects. These values did not differ significantly ($P = 0.71$). There was no significant difference in density estimates between the interior (19.1 ± 4.8 ind./km², $n = 180$) and edge transects (22.1 ± 4.8 ind./km², $n = 196$) for *E. rubriventer* ($P = 0.81$). For *H. g. griseus*, density estimates between the interior (7.8 ± 2.6 ind./km², $n = 72$) and edge transects (6.2 ± 2.1 ind./km², $n = 67$) did not differ significantly ($P = 0.56$). *A. laniger*, *E. rubriventer*, and *H. g. griseus* were classified as having a neutral edge response. The density of *M. rufus* was 12.5 ± 7.8 ind./km² ($n = 29$) for the interior transects, and 48.8 ± 9.0 ind./km² ($n = 95$) for the edge transects. These values differed significantly ($P = 0.01$). For *P. d. edwardsi*, density estimates between the interior (2.0 ± 0.8 ind./km², $n = 33$) and edge (7.3 ± 2.0 ind./km²,

TABLE I. Edge Responses for Six Lemur Species Compared Between Interior and Edge Transects in Vohibola III

Species	Number of individuals		Mean perpendicular distance (m) \pm 1 SD		Mean density (# individuals /km ²) and variance		Edge response
	Interior	Edge	Interior	Edge	Interior	Edge	
<i>A. laniger</i>	67	55	7.8 \pm 6.8	6.8 \pm 4.6	26.0 \pm 11.7	18.7 \pm 9.5	Neutral
<i>C. major</i>	59	23	5.6 \pm 2.8	7.0 \pm 4.1	23.4 \pm 9.9*	9.1 \pm 5.3*	Negative
<i>E. rubriventer</i>	180	196	9.5 \pm 8.0	8.7 \pm 6.3	19.1 \pm 4.8	22.1 \pm 4.8	Neutral
<i>H.g. griseus</i>	72	67	5.5 \pm 2.7	8.8 \pm 5.9	7.8 \pm 2.6	6.2 \pm 2.1	Neutral
<i>M. rufus</i>	29	95	6.0 \pm 3.8	4.6 \pm 3.3	12.5 \pm 7.8*	48.8 \pm 9.0*	Positive
<i>P. d. edwardsi</i>	33	65	15.0 \pm 10.4	9.8 \pm 8.7	2.0 \pm 0.8*	7.3 \pm 2.0*	Positive

* $P < 0.05$.

$n = 65$) transects also differed significantly ($P = 0.04$). Therefore, *M. rufus* and *P. d. edwardsi* were classified as having a positive edge response. Because *C. major* exhibited significantly lower ($P = 0.04$) density estimates in edge habitats (9.1 ± 5.3 ind./km², $n = 23$) compared to interior habitats (23.4 ± 9.9 ind./km², $n = 59$), this species was classified as having a negative edge response (Table I).

DISCUSSION

Neutral edge responses for *A. laniger* and *H. g. griseus* may occur because these species are largely folivorous [Faulkner, 2005; Tan, 1999]. Overdorff [1993] found that in *E. rubriventer* the percentage of feeding time spent on fruits was lowest from August to mid-October, but the percentage of feeding time spent on leaves was highest during July to mid-September. The abundance of leaves is unlikely to be influenced by edge effects [Norconk & Grafton, 2003]. However, edge-related variations in food quality, rather than abundance, represents a possible covariate to folivore distribution in Vohibola III. Ganzhorn [1995] documented that low-intensity logging increased light levels in western dry forests, which resulted in higher protein concentration in leaves. Elevated light levels have been documented near forest edges in Vohibola III [Lehman et al., in prep.]. Thus, we hypothesize that leaf quality may be highest near forest edges in Vohibola III. These edge-related variations in food quality are particularly relevant for *A. laniger*, which is a small-bodied (600–1,300 g) folivore with a simple monogastric stomach. *A. laniger* lacks two of the key morphological adaptations associated with folivory: large body size and a complex sacculated stomach [Faulkner, 2005]. If edges do contain higher-quality food sources for folivores, then the question arises as to whether *A. laniger* is edge tolerant throughout the year. Future studies will test this hypothesis by comparing the leaf chemistry of lemur food trees at differing proximities to forest edges. An interesting question that cannot be answered at this time is whether the neutral edge responses in *E. rubriventer* change during the time period of maximum fruit exploitation (ca. late November–early June).

M. rufus and *P. d. edwardsi* were classified as having a positive edge response in Vohibola III. Tolerance for edge effects by *M. rufus* may be due to the abundance of insect prey near the forest edge [Corbin & Schmid, 1995], although ecological patterns of insect abundance have not been studied directly in

southeast Madagascar. *M. rufus* tended to preferentially consume arthropods during the time period of this study [Atsalis, 1999]. Malcolm [1997] documented higher arthropod populations near forest edges, which explained why insectivorous mammals were not negatively influenced by edge effects in Brazil. Ultimately, detailed studies must be conducted on how edge effects influence the abundance and availability of insects eaten by lemurs in Vohibola III. The diverse diet of *P. d. edwardsi*—which includes seeds, fruit, and leaves—may enable it to exist in edge habitats [Hemingway, 1998]. However, because there are considerable intergroup variations in diet for *P. d. edwardsi* [Hemingway, 1998], understanding how this species responds to edge effects will require data on the feeding ecology of conspecifics in edge and interior habitats.

C. major exhibited a negative edge response that may be due to heightened ambient temperatures that inhibit torpor in edge habitats. *C. major* is thought to enter a torpid period between July and October [Petter et al., 1977]. Our research provides some support for this supposition in that sightings of *C. major* were made only between September and December. Moreover, we found that matrix temperatures penetrated up to 150 m in Vohibola III [Lehman, unpublished data]. Increased temperatures near forest edges have been shown to be inhibit torpor in *Microcebus murinus* and *Cheirogaleus medius* in dry forests [Ganzhorn & Schmid, 1998]. Overhunting in edge habitats may also influence *C. major* edge responses in Vohibola III.

Understanding lemur edge responses may explain how some species have survived dramatic habitat loss and forest fragmentation in Madagascar. In the light of theoretical work on thresholds of forest loss and fragmentation, it is surprising that recent (i.e., within the last 50 years) landscape changes have not resulted in any lemur extinctions [Fahrig, 2002], although there have been many extirpations of extant taxa [Godfrey et al., 1999]. *A. laniger*, *H. g. griseus*, and *E. rubriventer* may not be the only tropical taxa that are unaffected by edge effects. Malcolm [1997] found that the abundance of many species of arboreal mammals was not affected by forest fragmentation, matrix conditions, or edge effects in Brazil. However, lemurs that exhibit positive edge responses may ultimately experience higher hunting pressures by local people [Ries & Fagan, 2003]. Although local people rarely hunt lemurs in Vohibola III [Lehman et al., in press], increased hunting pressure may occur near forest edges. For example, Lehman and Wright [2000] found that most lemur snare traps were in close proximity to forest edges at two sites 30 km north of Vohibola III. Therefore, positive edge responses in *M. rufus* and *P. d. edwardsi* may be beneficial in terms of their ecology, but detrimental in terms of their interactions with humans.

Increased sample sizes for surveys, as well as data on food abundance and quality, will help us achieve a greater understanding of how lemurs respond to edge effects. Ongoing surveys should provide sufficient data to describe edge responses for other lemur taxa (e.g., *Eulemur fulvus rufus* and *Lepilemur microdon*) in Vohibola III. We are also investigating how synergistic edge effects (e.g., hunting and tree species composition) covary with lemur population dynamics. Finally, data are needed regarding how forests and lemurs are being influenced by edge effects in other biogeographic regions in Madagascar.

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