



Edge effects and extinction proneness in a herpetofauna from Madagascar

RICHARD M. LEHTINEN^{1,*}, JEAN-BAPTISTE RAMANAMANJATO^{2,3} and JOÉ GABY RAVELOARISON³

¹Museum of Zoology, Division of Reptiles and Amphibians, University of Michigan, 1109 Geddes Avenue, Ann Arbor, MI 48109-1079, USA; ²QIT Madagascar Minerals S.A., B.P. 225, 614 Fort-Dauphin, Madagascar; ³Departement de Biologie Animale, Université d'Antananarivo, 101 Antananarivo, Madagascar; *Author for correspondence (e-mail: rmllehtin@umich.edu; fax: +1-734-763-4080)

Received 28 January 2002; accepted in revised form 10 July 2002

Key words: Amphibians, Edge effects, Extinction, Habitat fragmentation, Madagascar, Matrix, Reptiles

Abstract. Edge effects are thought to play a key role in fragmented habitats. It is often assumed that edge-avoiding species are more prone to local extinction than non-edge-avoiding species, but there are few data to support this assumption. Also, few data are available on the effects of edges on some groups, and there is little understanding of seasonal changes in edge effect intensity. To better understand the role that edge effects play in fragmented tropical forests, we assessed the distribution of reptiles and amphibians in six littoral rainforest fragments in southeastern Madagascar in 1999 (dry season) and 2000 (wet season). Using randomization tests, we found all three types of edge responses: edge-avoiders, interior-avoiders, and omnipresent species. However, edge responses varied considerably among seasons. For example, some species (e.g., *Mantidactylus bicalcaratus*, *Phelsuma quadriocellata*) were strong edge-avoiders in the dry season, but showed no preference for edge or interior habitats during the wet season. Also, edge-avoiding species tended to be more extinction-prone than non-edge-avoiding species. Abiotic data documented significantly higher temperatures and dew point temperatures near edges. Wind speed also tended to be higher and relative humidity tended to be lower near edges. Our results indicate that many amphibians and reptiles respond to altered microclimates near edges and these responses have a strong seasonal component. For many species, edge sensitivity does seem to be correlated with extinction vulnerability and therefore should be of primary consideration in plans to conserve biodiversity in fragmented tropical forests.

Introduction

The island of Madagascar has a remarkably diverse and unique biota due to its long period of isolation from other landmasses. The Malagasy herpetofauna is no exception, as 99% of the amphibians and 90% of the reptiles are endemic (Glaw and Vences 1994). Much of this diversity is still being uncovered, and consequently, very little is known about the conservation status of these species. Unfortunately, rates of forest loss in Madagascar are nearly as high as the levels of endemism. Satellite imagery, now over 10 years old, indicates that at least 90% of the original forests have been lost (Green and Sussman 1990). In short, there is a great need for scientific information to guide the conservation of this unique and poorly known biota.

In Madagascar, as in many areas of the world, habitat loss is proceeding at such a rate that many habitats will persist only in relatively small, isolated fragments (Whitmore 1997). The altered areas that surround fragments (often termed the matrix) generally have distinctly different environmental characteristics than the fragments themselves and the interactions between the matrix and the fragments are termed edge effects (Murcia 1995). A dramatic increase in the proportion of edge in remnant habitats is a conspicuous feature of fragmented landscapes.

The altered environmental conditions found near the interface between the matrix and fragments include modified wind, moisture or temperature regimes, increases in solar radiation penetration, and changes in vapor pressure deficits (Williams-Linera 1990; Chen et al. 1992; Matlack 1993; Camargo and Kapos 1995; Turton and Freiburger 1997; Stevens and Husband 1998). This altered environment near the edge often influences the biota inhabiting fragments. For example, edge conditions can cause changes in the distribution and abundance of individuals in fragments (e.g., Esseen and Renhorn 1998). The influence of these microclimatic changes often diminishes monotonically towards the interior of fragments, but more complex patterns are known (Kapos et al. 1997).

Edge effects are increasingly seen as very important to persistence in fragmented landscapes (Laurance 1999). In small fragments, where a large proportion of the habitat is edge, edge effects may reduce the amount of suitable 'core' habitat for interior species to the point where extinction is likely. This connection between edge-avoidance and extinction vulnerability in fragmented landscapes is often assumed (either explicitly or implicitly), but has rarely been demonstrated empirically (Laurance 1999). Species that do not avoid edges, on the other hand, are more likely to be unaffected by, or benefit from, edge effects. Edge effects will often be important in interpreting patterns of biodiversity loss in fragmented landscapes and should be taken into account in conservation planning. However, in a recent review, Murcia (1995) concluded that little could be generalized from the often conflicting results of the studies conducted due to methodological differences and a lack of appreciation for the spatial and temporal complexities of edge effects.

Relatively few studies have examined edge effects in amphibians and reptiles, despite the expectation that these organisms might respond strongly to edges because of physiological needs. For example, changes in temperature regimes near edges would be expected to alter the distribution of many reptiles and amphibians because of their reliance on the environment to provide body heat (ectothermy). Therefore, amphibians and reptiles are predicted to respond behaviorally to edges for thermoregulatory purposes. In addition, amphibians respire primarily through their moist skin and may be more vulnerable to desiccation in drier environments near edges. If this is the case, we would expect amphibians to exhibit seasonal responses to edges that correspond to rainfall patterns.

We surveyed a herpetofauna in southeastern Madagascar to quantify the role that edge effects play in a fragmented landscape. Our objectives were: (1) to document whether the proximity of edges significantly alters the distribution of amphibian and reptile species in fragments. (2) To document whether these patterns vary seasonally. (3) To test if changes in the distribution of amphibians and reptiles are correlated

with changes in the abiotic environment near edges. (4) To test if edge-avoiding species are more extinction-prone than species which do not avoid edges. Since habitat loss and fragmentation have been implicated as primary causes in declines of amphibians and reptiles (Pechmann and Wilbur 1994; Raxworthy and Nussbaum 2000), it is important to further our understanding of how these groups are impacted by habitat fragmentation.

Methods

Study area

We conducted this study in southeastern Madagascar at Mandena ($24^{\circ}57' S$, $47^{\circ}02' E$) and Sainte Luce ($24^{\circ}46' S$, $47^{\circ}10' E$), which are approximately 10 and 30 km north of Tolagnaro (Fort-Dauphin), Toliara fivondronana, respectively (Figure 1). This area was historically littoral (coastal) rainforest, a rare forest type in Madagascar. Malagasy littoral rainforest is found in a narrow coastal strip between the Indian Ocean and the highlands to the west. It resembles higher altitude rainforest further inland, but is only found on sandy soils at very low elevations and contains numerous endemic species (Goodman et al. 1997). Rainfall in this area averages 1500–2000 mm annually, with most rain falling between November and April (Koechlin 1972; Goodman et al. 1997).

At present, the landscape at Mandena and Sainte Luce is a series of littoral rainforest fragments in a matrix of extremely degraded anthropogenic sand-scrub. This barren sand-scrub is the result of previous forest clearing, burning, and attempts at cattle grazing and is presumably a hostile environment for forest-

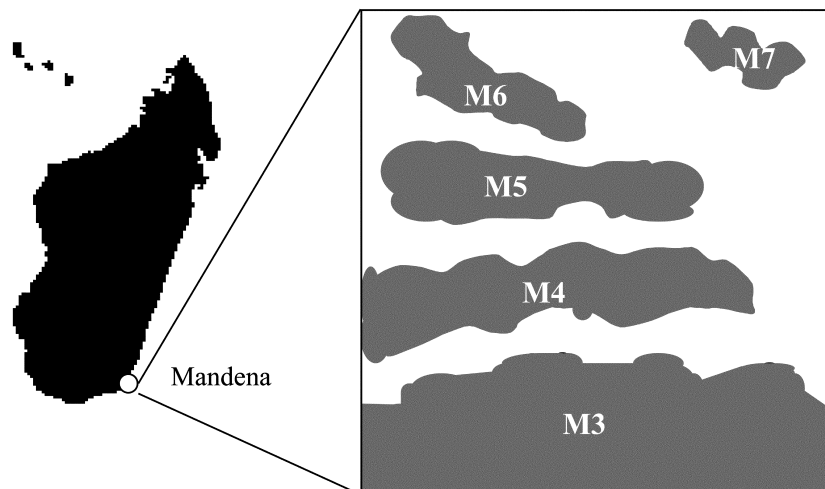


Figure 1. Location of the study site in southeastern Madagascar and map of sampled fragments at Mandena (not to scale – Sainte Luce is not pictured).

Table 1. Characteristics and sampling effort among six study fragments.

| Fragment name | Location | Size (ha) | No. of edge transects |
|---------------|-------------|-----------|-----------------------|
| S9 | Sainte Luce | 457 | 29 |
| M3 | Mandena | 221 | 23 |
| M4 | Mandena | 41 | 17 |
| M5 | Mandena | 28 | 12 |
| M6 | Mandena | 20 | 9 |
| M7 | Mandena | 10 | 6 |

dwelling organisms. The remaining forest is under considerable human pressure and is heavily utilized by locals for fuel wood, building materials, and other forest products (R. Lehtinen, personal observation). These fragments have been classified as slightly to moderately degraded based on botanical surveys and have been isolated for at least 50 years. For additional information on the study area see Ramanamanjato (2000).

Of the remaining littoral rainforest fragments in the area, we selected six for this study (designated M3, M4, M5, M6, M7 and S9). Study fragments ranged in size from 10 to 457 ha (Table 1). Elevation varied between 0 and 20 m above sea level, and all fragments were located in a sand-scrub matrix. All sampled edges were 'hard' edges, that is, there was an abrupt transition between forest and matrix habitats. No detailed information was available on edge age. However, due to fire, cattle grazing, and harvesting pressure, these forest edges could be termed 'retreating edges' because of continual disturbance and encroachment. The vegetation seal often found at older edges (Murcia 1995) was rarely present and these edges are probably best classified as young (<5 years).

Survey techniques

We used transects 50 m long and 6 m wide to sample amphibians and reptiles. All transects were oriented perpendicular to the fragment edge and located entirely within the forest habitat. We defined the starting point for all transects as the first woody vegetation >2 m in height that was fully exposed on one side to matrix habitat. All transects were placed at least 50 m from the nearest other transect and were searched starting at the edge. Transects of 50 m were used because longer transects could not be used in some of the smaller fragments without approaching the opposite edge. This is also within the range that edge effects have been detected in previous studies (e.g., Demaynadier and Hunter 1998).

Amphibians and reptiles were detected along transects using visual and auditory cues. While searching transects, we examined likely refugia, such as tree holes, the leaf axils of screw pines (*Pandanus*), under the bark of dead trees, or in the leaf litter. For each detection along the 50 m transects, three pieces of information were recorded: species identity, distance from the fragment edge (m), and microhabitat data. Microhabitat data included a description of the capture point (e.g., under log, in leaf litter) and an estimate of canopy cover. Captured animals were not marked; therefore, each transect was sampled only once in each season to preserve the

independence of observations. Two or three individuals searched each transect and survey time per transect varied from 41 to 70 min. Ninety-six 50 m transects were sampled during this study (48 during the day and 48 at night, with proportionally more transects in larger fragments; Table 1), totaling over 358 person-hours of survey time. Sampling was conducted during the day (7.00 A.M.–16.00 P.M.) and at night (19.00 P.M.–1.00 A.M.) with the aid of headlamps. Transect sampling occurred from 31 May to 21 June 1999 (dry season – Mandena) and from 21 February to 28 March 2000 (wet season – Mandena and Sainte Luce). Although the matrix was not systematically surveyed, several species were frequently detected while traveling between fragments and are referred to as matrix associated species in subsequent tables.

Most amphibians and reptiles in this area are found on the forest floor or in arboreal habitats. However, some species are found in the water-filled leaf axils of screw pines (*Pandanus*). Because *Pandanus* provide a unique aquatic microhabitat for some amphibians and reptiles (R. Lehtinen, unpublished data), we quantified the spatial distribution of these plants along our transects. These data were used to assess the possibility that *Pandanus* (rather than the amphibians and reptiles that inhabit them) are less likely to occur near edges. Cover objects (e.g., logs, stumps) were also quantified along transects for this purpose.

All individuals were identified in the field and either released or retained as reference specimens. Reference specimens for all species were deposited at the University of Michigan Museum of Zoology (UMMZ 226968-227000) and the Department de Biologie Animale at the Université d'Antananarivo, Madagascar. At least two *Lygodactylus* species were captured (*L. miops* and *L. tolampye*) but were lumped in all analyses because of difficulties in field identification. Also, the taxon *Mantidactylus boulengeri* may contain an undescribed sister species in this area that is morphologically very similar (Glaw and Vences 1994). These two forms were likewise lumped in all analyses. The total species pool of amphibians and reptiles summed over all forest fragments in the study area has been estimated at 69 species (Ramanamanjato 2000; R. Lehtinen, unpublished data). Nomenclature generally follows Glaw and Vences (1994).

Abiotic data collection

Two datasets (one short-term, one long-term) were collected on the environmental conditions near forest edges. The short-term data were collected along three 50 m transects established in fragment S9. Data on temperature (°C), relative humidity (%), dew point temperature (°C) and wind speed (m/s) were collected every 10 m along each transect using a Kestrel 3000 weather meter (Nielsen-Kellerman, Co., Chester, Pennsylvania). The weather meter was hung on a branch 1.0 m off the ground, out of direct sunlight, 2.0 m away from the observer. Data were recorded after 90 s at each point, to allow readings to stabilize. Wind speed was the maximum wind speed recorded at each point during the 90 s period. Transects were separated by at least 100 m and were sampled in random order between 11.00 A.M. and 15.00 P.M. on 7 days between 17 February 2002 and 1 March 2002 (rainy season). Data

accuracy was $\pm 3\%$ for wind speed and humidity and ± 1.0 °C for temperature and dew point temperature.

The long-term dataset includes temperature data collected with two data loggers (HOBO model Pro Temp) installed at 1.0 m height at 20 and 400 m from the edge of fragment S9. Temperatures were recorded every 2 h from 1 December 1999 to 24 March 2000 (wet season). Data accuracy was ± 0.4 °C.

Statistical analysis

Randomization techniques were used to test the null hypothesis that a species was distributed randomly along edge-to-interior transects. This involved calculating a mean distance of detection from the observed values pooled among fragments for each species. Then, an equivalent number of values between 0 and 50 were randomly generated. This procedure was repeated 1000 times to create a statistical distribution in which to compare the observed values. The number of times a mean value equal to or more extreme than the observed mean was found indicates how probable that distribution of values was under the null hypothesis of randomly distributed detections (Manly 1997). We assumed that, given a large enough sample, a species that did not respond to edge proximity would have a mean detection distance that converges on 25 m. When a significant result was detected ($P < 0.05$), the species was classified as an edge-avoider or an interior-avoider, depending on whether the mean distance was above or below 25 m. Non-significant results were classified as omnipresent species.

For example, the gecko *Ebenavia inunguis* was detected 11 times during the 2000 wet season at the following distances from the fragment edge (14, 17, 27, 11, 6, 28, 3, 26, 50, 20, and 13 m; mean = 19.6 m). To test whether this particular sample of values differed from random, the randomization technique randomly selected 11 values between 0 and 50 and calculated a mean. This procedure was then repeated 999 additional times. For *E. inunguis*, 124 out of the 1000 randomizations had a mean value less than or equal to the observed mean of 19.6 m ($P = 0.124$, one-tailed probability). At $\alpha = 0.05$, this is not enough evidence to reject our null hypothesis and the result is considered non-significant. Therefore, *E. inunguis* was classified as omnipresent in the 2000 wet season.

Data from different fragments were pooled after preliminary analyses indicated similar patterns among fragments. When sample sizes permitted, separate randomization tests were run for dry season and wet season data. Bonferroni correction for multiple tests was unnecessary, as the data for each species and season were tested only once. Only those species with five or more detections were analyzed with this technique. When multiple individuals of the same species were found at the same capture point (e.g., *Pandanus* leaf axils), a single data point was recorded. Randomization tests were used instead of more standard statistical techniques because they are robust to small sample sizes and they require no assumptions regarding the underlying distribution of the data (Manly 1997). An identical technique was used to examine the influence of canopy cover and the distribution of *Pandanus* plants

Table 2. Results of randomization tests for edge preferences.

| Species | 1999 (dry season) | | | | 2000 (wet season) | | | | Seasonal difference? | No. of local extinctions |
|--|----------------------|---------------------|------|-----------------|----------------------|---------------------|------|-----------------|-------------------------|-----------------------------|
| | <i>n</i> | Edge dist (m) | SD | <i>P</i> -value | <i>n</i> | Edge dist (m) | SD | <i>P</i> -value | | |
| | Reptiles | | | | | | | | | |
| <i>Amphiglossus macrocercus</i> | 4 | 21.8 | 9.9 | – | – | – | – | – | – | 3 |
| <i>Amphiglossus melanopleura</i> | 7 | 33.4 | 17.0 | 0.056 | 3 | 44.0 | 7.9 | – | – | 1 |
| <i>Amphiglossus ornaticeps</i> | 18 | 29.3 | 17.2 | 0.103 | 2 | 15.0 | 17.0 | – | – | 0 |
| <i>Brookesia nasus</i> | – | – | – | – | 2 | 18.5 | 7.8 | – | – | 4 |
| <i>Ebenavia inunguis</i> | 4 | 31.0 | 17.6 | – | 11 | 19.6 | 13.1 | 0.124 | – | 2 |
| <i>Furcifer lateralis</i> | 4 | 9.3 | 8.2 | – | 12 | 28.7 | 13.6 | 0.194 | – | 0 |
| <i>Furcifer oustaleti</i> | 7 | 13.7 | 9.9 | 0.019* | 2 | 28.0 | 31.1 | – | – | 0 |
| <i>Geckolepis maculata</i> | – | – | – | – | 5 | 10.8 | 10.2 | 0.014* | – | 2 |
| <i>Hemidactylus mercatorius</i> | 52 | 22.8 | 15.8 | 0.146 | 18 | 24.4 | 15.2 | 0.449 | N | 0 |
| <i>Ithycyphus oursi</i> | – | – | – | – | 1 | 46.0 | – | – | – | 2 |
| <i>Liophidium torquatum</i> | 2 | 26.0 | 33.9 | – | – | – | – | – | – | 2 |
| <i>Liopholidophis lateralis</i> ^a | – | – | – | – | 2 | 1.5 | 0.7 | – | – | 1 |
| <i>Lygodactylus</i> sp. | 44 | 31.6 | 13.8 | < 0.001*** | 175 | 25.6 | 14.2 | 0.313 | Y | 0 |
| <i>Mabuya elegans</i> ^a | 13 | 2.6 | 5.5 | < 0.001*** | 15 | 17.9 | 12.4 | 0.024* | N | 0 |
| <i>Mabuya gravenhorstii</i> | 5 | 21.8 | 24.1 | 0.298 | 31 | 24.8 | 15.7 | 0.5 | N | 0 |
| <i>Madagascarophis colubrinus</i> | 2 | 36.0 | 0.0 | – | 5 | 32.8 | 10.0 | 0.125 | – | 1 |
| <i>Mimophis mahfalensis</i> ^a | 1 | 0.0 | – | – | 3 | 36.0 | 10.4 | – | – | 0 |
| <i>Phelsuma lineata</i> | 24 | 24.6 | 16.9 | 0.44 | 16 | 20.0 | 12.3 | 0.06 | N | 2 |
| <i>Phelsuma modesta</i> | 25 | 34.6 | 13.9 | 0.001** | 46 | 28.6 | 14.2 | 0.045* | N | 0 |
| <i>Phelsuma quadriocellata</i> | 15 | 36.7 | 13.3 | < 0.001*** | 54 | 25.4 | 14.9 | 0.403 | Y | 2 |
| Amphibians | | | | | | | | | | |
| <i>Anodontohyla boulengeri</i> | – | – | – | – | 2 | 18.0 | 11.3 | – | – | 3 |
| <i>Heterixalus boettgeri</i> ^a | 23 | 30.4 | 15.9 | 0.039* | 17 | 17.2 | 15.4 | 0.013* | Y | 0 |
| <i>Mantidactylus betsileanus</i> | 10 | 33.9 | 14.4 | 0.028* | – | – | – | – | – | 2 |
| <i>Mantidactylus bicalcaratus</i> | 15 | 36.8 | 16.6 | 0.001** | 107 | 26.4 | 15.4 | 0.147 | Y | 3 |
| <i>Mantidactylus boulengeri</i> | 18 | 32.4 | 15.0 | 0.016* | 164 | 30.4 | 13.9 | < 0.001*** | N | 1 |
| <i>Mantidactylus depressiceps</i> | 21 | 31.9 | 14.5 | 0.019* | 7 | 31.8 | 17.6 | 0.098 | Y | 2 |
| <i>Mantidactylus domerguei</i> ^a | – | – | – | – | 3 | 3.0 | 1.9 | – | – | 1 |
| <i>Mantidactylus punctatus</i> | 20 | 33.4 | 15.7 | 0.005** | 60 | 26.5 | 14.8 | 0.187 | Y | 3 |
| <i>Ptychadena mascariensis</i> ^a | – | – | – | – | 7 | 18.9 | 16.0 | 0.158 | – | 0 |

Data from dry season 1999 and wet season 2000 data are listed separately. Minimum observations for analysis, $n = 5$. Edge distance is the mean of all edge proximity measurements. Number of local extinctions is the number of sampled fragments from which a species is absent (out of six; see text for details). * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$; ^aMatrix-associated species.

and cover objects along transects. Randomization tests were designed using a macro in Microsoft Excel.

Linear regression was used to test the hypothesis that edge-avoiding species were more extinction-prone than non-edge-avoiding species. For this analysis, the independent variable was the mean distance from the edge for each species during the dry season (1999) and the dependent variable was extinction proneness (quantified by the number of absences among the sampled fragments – Ramanamanjato 2000;

R. Lehtinen, unpublished data). Regressions were calculated for all species pooled and for amphibians and reptiles separately.

Short-term abiotic transect data were analyzed using mean values for temperature, relative humidity (arcsine transformed), dew point temperature and wind speed as dependent variables in one-way analyses of variance using edge distance as a factor. If ANOVAs were significant, Bonferroni post-hoc comparisons were used to determine which treatments (edge distances) were different. Long-term temperature data were analyzed using a *t*-test to examine differences in mean daily temperature.

Results

During this study, 1105 individuals of 30 species were captured (Table 2), a little less than 50% of the known herpetofauna in the study area. Twenty-one species had enough data to analyze for edge preferences. Three different types of edge responses were observed: interior-avoiders (tending to be found at or near edges), edge-avoiders (tending to be found toward the interior), and omnipresent species (no significant preference for edge or interior habitats; Table 2).

Dry season (1999) data revealed that all frogs were significant edge-avoiders (six species – Table 2). Reptiles had more varied responses with some species significantly preferring edges (e.g., *Mabuya elegans*, *Furcifer oustaleti*), some preferring interior areas (e.g., *Lygodactylus* sp., *Phelsuma modesta*, *P. quadriocellata*) and others showing no preference (e.g., *Hemidactylus mercatorius*, *Amphiglossus ornaticeps*).

Data from the wet season (2000) revealed different patterns. Among frogs, *Mantidactylus boulengeri* remained an edge-avoiding species, but all other species either showed no significant response to edge proximity (e.g., *Mantidactylus bicalcaratus*, *M. depressiceps*, *M. punctatus*) or were interior avoiders (*Heterixalus boettgeri*). No reptiles were significant edge-avoiders during the wet season. Three species, however, were significant interior-avoiders (*Mabuya elegans*, *Phelsuma lineata*, and *Geckolepis maculata*). All other reptiles for which there were more than five observations were omnipresent relative to edge proximity in the wet season (Table 2).

Six species were detected both in the forest fragments and the matrix surrounding the fragments (*Liopholidophis lateralis*, *Mabuya elegans*, *Mimophis mahfalensis*, *Heterixalus boettgeri*, *Mantidactylus domerguei*, and *Ptychadena mascarieniensis*; Table 2). Closely related species sometimes had similar responses to edge proximity (e.g., *Mantidactylus bicalcaratus* and *M. punctatus* were edge-avoiders in the dry season and omnipresent in the wet season). In many cases, however, edge responses among closely related species were markedly different (e.g., *Mabuya elegans* – consistent interior-avoider; *Mabuya gravenhorstii* – consistently omnipresent).

Two frog species (*Mantidactylus bicalcaratus* and *M. punctatus*) were only found in the leaf axils of screw pine (*Pandanus*) plants (202 total captures). Other species facultatively occupied the leaf axils of *Pandanus*, including: *Phelsuma lineata*, *P. quadriocellata*, *Mantidactylus depressiceps* and *Heterixalus boettgeri* (R. Lehtinen,

unpublished data). Randomization tests of *Pandanus* distributions failed to reject the null hypothesis that these plants are randomly distributed along transects ($P = 0.306$, $n = 71$). Randomization tests of the distribution of cover objects also could not refute the hypothesis of a random distribution ($P = 0.571$, $n = 142$). Analyses of species distributions in relation to canopy cover were not revealing and are not reported here.

While some species clearly do not fit the pattern, the results of linear regression analysis indicate that there is a significant positive relationship between strength of edge-avoidance and extinction vulnerability (all species; $r^2 = 0.473$; $P = 0.026$; Figure 2). This relationship is marginally significant when considering only amphibians ($r^2 = 0.744$; $P = 0.055$) and non-significant for reptiles only ($r^2 = 0.389$; $P = 0.136$; Figure 2).

Analysis of abiotic transect data (Figure 3) indicated significant differences among treatments (edge distances) for temperature ($F_{5,12} = 15.01$, $P < 0.001$) and dew point temperature ($F_{5,12} = 8.33$, $P = 0.001$). Post-hoc comparisons indicated that measurements taken at the edge gave significantly higher temperature and dew point temperature than more interior transect locations (Figure 3). Relative humidity was marginally significant ($F_{5,12} = 3.05$, $P = 0.052$) and wind speed was non-significant ($F_{5,12} = 1.45$, $P = 0.276$). However, as with temperature and dew point temperature, a trend was evident for lower relative humidity and higher wind speeds near the edge (Figure 3). In addition, significant differences were detected in edge

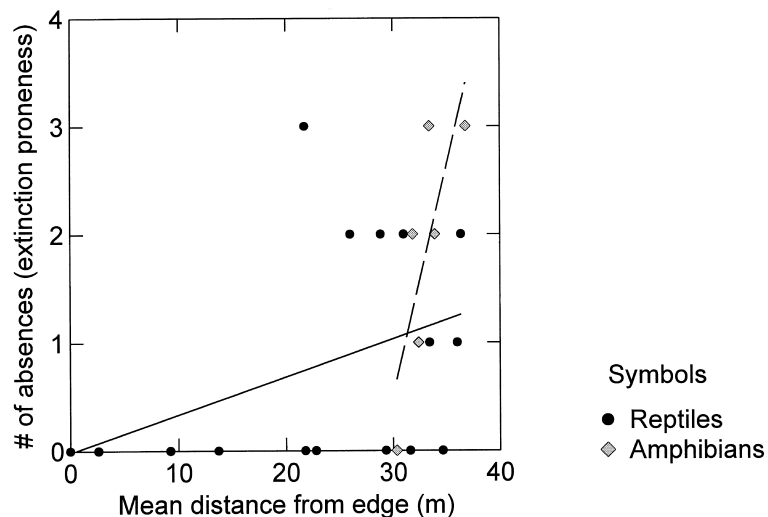


Figure 2. The number of observed absences (local extinctions) of each species versus the mean distance from the edge (m) along 50 m transects in the dry season (1999). Linear regression lines are for frogs only (dashed; $r^2 = 0.744$; $P = 0.055$; $n = 6$) and reptiles only (solid; $r^2 = 0.389$; $P = 0.136$; $n = 16$). Regression of all species pooled was significant ($r^2 = 0.473$; $P = 0.026$; $n = 22$). Circles indicate reptiles, diamonds indicate frogs.

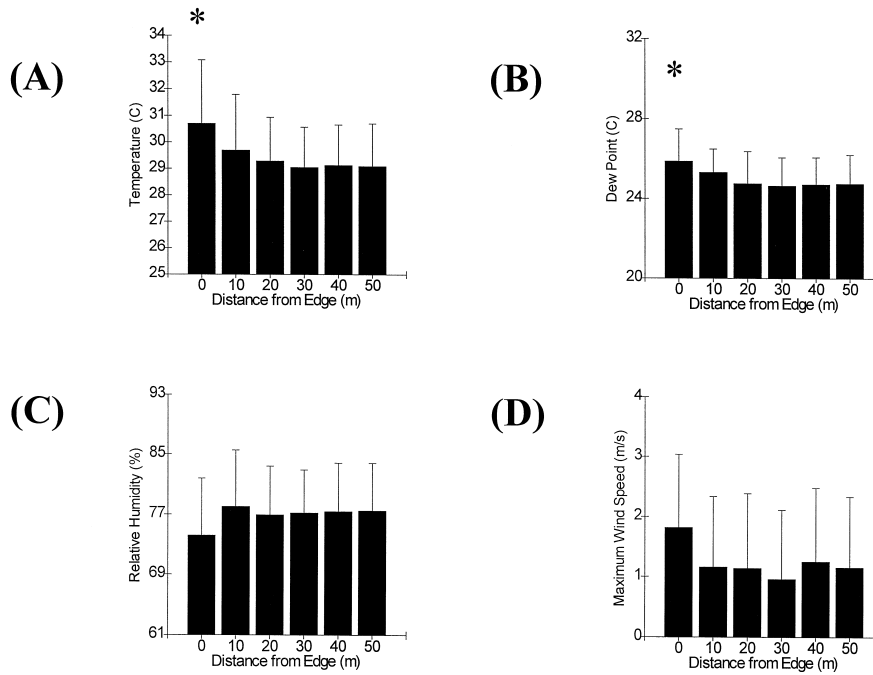


Figure 3. Edge distance (m) versus (A) temperature (°C), (B) dew point temperature (°C), (C) relative humidity (%) and (D) maximum wind speed (m/s). Data are from three transects in fragment S9, rainy season 2002. Significant differences are indicated by an asterisk (*).

and interior temperatures from the long-term abiotic data (t -test, $n = 1363$, $P < 0.0001$; Figure 4).

Discussion

Edge proximity influenced the distribution of many species in this study. Some species responded to edge environments by inhabiting only the interior core of the fragments (edge-avoiders). Other species preferred the areas near the edge (interior-avoiders). For many edge-avoiding species, edge effects were detectable in the form of altered distributions at least 30 m into the forest. Further, these results are conservative as areas beyond 50 m towards the interior were not sampled.

However, the impact of edge proximity differed greatly between the wet and dry seasons. Some species that avoided edges in the dry season did not avoid edges in the wet season (e.g., *Mantidactylus bicalcaratus*, *Lygodactylus* sp.; Table 2). This seasonal variability in the severity of edge effects was presumably due to increases in temperature and rainfall in the hot, wet season. In other seasonal environments, similar changes in edge responses may be obscured if studies are conducted only during a certain time of year or if data from different seasons are pooled together. As

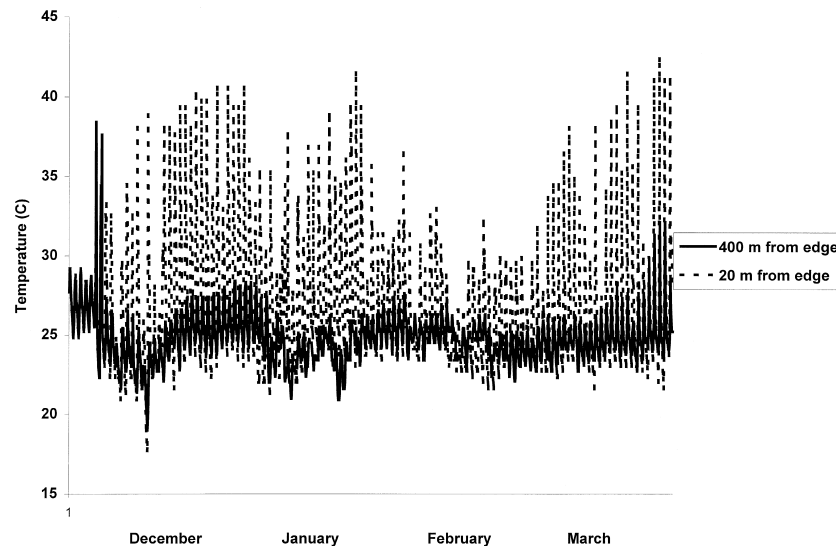


Figure 4. Temperature ($^{\circ}\text{C}$) data from fragment S9 (1 December 1999 – 24 March 2000), 20 m from edge and 400 m from edge. Mean daily temperature ($^{\circ}\text{C}$) is significantly higher 20 m from the edge than in the forest interior (t -test, $P < 0.0001$).

suggested by Schlaepfer and Gavin (2001), seasonally variable responses to edges, while infrequently reported, are probably the norm rather than the exception.

The strong seasonal response to edges in frogs in this study is consistent with the suggestion that many amphibians are sensitive to edge effects during dry periods (Demaynadier and Hunter 1998; Gibbs 1998). The physiological constraints of a highly permeable skin that needs relatively cool, moist conditions for proper respiration, may predispose many amphibians to avoid edge habitats. One frog in this study, *M. boulengeri*, was a significant edge-avoider in both the wet and dry seasons. In contrast to the other frogs, this species is thought to lay its eggs terrestrially in the wet season (Glaw and Vences 1994; R. Lehtinen, unpublished data). These eggs would be particularly vulnerable to desiccation and, even in the rainy season, this species avoids edges. Another frog, *Heterixalus boettgeri*, breeds during the wet season in sun-exposed swamps in the matrix but in the dry season these frogs move back into forests (R. Lehtinen, unpublished data). These life history events are reflected in its edge preferences (dry season – edge-avoider; wet season – interior-avoider, Table 2). These examples highlight the importance of life history patterns in explaining differences in edge sensitivity.

Screw pines (*Pandanus*) are important microhabitats for some species in this system. The leaf axils of these plants remain water-filled, or at least damp, throughout the year and seem to be used as refugia from drying conditions. Several species of frogs are obligate *Pandanus*-dwellers throughout their life cycle, while other species use *Pandanus* facultatively during dry periods (R. Lehtinen, unpublished data). The result that *Pandanus* are randomly distributed, yet the species

that inhabit them are often not (Table 2), indicates that edge responses in *Pandanus*-inhabiting species cannot be explained by a decrease in abundance of these plants near edges. Similarly, the distribution of cover objects was indistinguishable from random and therefore had minimal bias on our inferences of edge effects.

Our data indicate that edge-avoiding amphibians and reptiles tend to be more prone to local extinction in fragments than those that do not avoid edges (Figure 2). The converse was also generally true: most interior-avoiding or omnipresent species were extinction resistant. However, some species do not fit this pattern (e.g., *Phelsuma modesta*, *Lygodactylus* sp.) and there was substantial variability among groups. This differential extinction vulnerability may be due to species or group-specific traits, such as cutaneous respiration in amphibians. Frogs were particularly likely to be both edge-avoiding and extinction-prone. This finding could help explain losses of amphibians from fragmented systems (Marsh and Pearman 1997; Vallan 2000) and may play a significant role in amphibian declines.

Up to this point, we have assumed that edge responses of the amphibians and reptiles in this study were in response to altered microclimatic conditions near the edge. Both our short-term abiotic transect data and the long-term temperature data support this assumption. While only temperature and dew point temperature showed significant differences along the edge transects, all variables measured in the short-term dataset showed a trend of altered conditions near the edge (Figure 3). Since these data are from the rainy season, we would expect edge microclimates to be further altered in the dry season. Our long-term temperature data also indicate that edge environments have warmer and more variable microclimates than interior areas (Figure 4). From these two sources of evidence, it seems likely that it is these altered abiotic conditions near the edge that are influencing the spatial distribution of amphibians and reptiles in this study.

Our results are consistent with previous studies on amphibians and reptiles that have shown that these organisms are often sensitive to conditions at fragment edges (e.g., Gambold and Woinarski 1993; Pearman 1997; Demaynadier and Hunter 1998; Sartorius et al. 1999). Similar to Gascon (1993) and Schlaepfer and Gavin (2001), we found that responses to edges are less obvious during wet periods and that edge responses are often highly dynamic in space and time.

Species associated with the matrix were rarely found to avoid edges (Table 2). In fact, most matrix species for which there was sufficient data appeared to be interior-avoiders (e.g., *Mabuya elegans*, *Ptychadena mascareniensis*). Matrix-associated species are frequently the most extinction resistant species in fragmented landscapes (see Table 2) and matrix tolerance may often be inversely correlated with edge sensitivity (Gascon et al. 1999). However, this relationship will depend, in part, on the degree of contrast between the matrix and the fragment (Mesquita et al. 1999). Preliminary data from other fragments in this area in an *Eucalyptus* plantation matrix indicate that the intensity of edge effects may be reduced under different matrix conditions (R. Lehtinen and J.G. Raveloarison, unpublished data). This suggests that management of the matrix (rather than just the fragments themselves) can benefit edge-avoiding species in fragmented landscapes.

Less than 50% of the known herpetofauna in this area was detected during this

study. Many of the species not detected are rare or are known to only occur in fragments that we did not sample (Ramanamanjato 2000). Particularly, snakes and fossorial frogs and lizards were probably undersampled with our transect methodology. Also, differences in the number of individuals observed per species among seasons were often considerable (Table 2) and may be attributable to sampling error or to differences in detectability. It is possible that a sampling bias exists from starting all transects at the edge and moving towards the interior, but the existence or strength of any such bias is unknown. The degree to which degradation in these fragments has contributed to the observed patterns is also unknown.

This study has empirically demonstrated that proximity to altered edge microclimates influences the distribution of many amphibians and reptiles in forest fragments and that these effects have a strong seasonal component. We have also shown that edge-avoiding species tend to be more extinction-prone than non-edge-avoiders. Clearly, explaining patterns of biodiversity loss in fragmented landscapes must include a consideration of edge effects. However, to fully understand the way in which mobile organisms respond to edges in fragmented systems, relatively long-term abiotic and biotic monitoring as well as a detailed knowledge of matrix conditions and natural histories will be necessary.

Acknowledgements

We thank QIT Madagascar-Minerals S.A. for permission to conduct this study at Mandena and Sainte Luce. Numerous locals helped in the field. Les Directions des Eaux et Forêt in Antananarivo provided permission to conduct research and collect reference specimens. R. Nussbaum and G. Schneider provided assistance at UMMZ. Several anonymous reviewers provided useful comments that improved this manuscript. This project was funded by grants from the Horace H. Rackham Graduate School, the Department of Ecology and Evolutionary Biology, the International Institute and the Museum of Zoology at the University of Michigan.

References

- Camargo J.L.C. and Kapos V. 1995. Complex edge effects on soil moisture and microclimate in central Amazonian forest. *Journal of Tropical Ecology* 11: 205–221.
- Chen J., Franklin J.F. and Spies T.A. 1992. Vegetation responses to edge environments in old-growth Douglas-fir forest. *Ecological Applications* 2: 387–396.
- Demaynadier P.G. and Hunter M.L. Jr 1998. Effects of silvicultural edges on the distribution and abundance of amphibians in Maine. *Conservation Biology* 12: 340–352.
- Esseen P.A. and Renhorn K.E. 1998. Edge effects on an epiphytic lichen in fragmented forests. *Conservation Biology* 12: 1307–1317.
- Gambold N. and Woinarski J.C.Z. 1993. Distributional patterns of herpetofauna in monsoon rainforests of the Northern Territory, Australia. *Australian Journal of Ecology* 18: 431–449.
- Gascon C. 1993. Breeding-habitat use by five Amazonian frogs at forest edge. *Biodiversity and Conservation* 2: 438–444.

- Gascon C., Lovejoy T.E., Bierregaard R.O. Jr, Malcolm J.R., Stouffer P.C., Vasconcelos H.L. et al. 1999. Matrix habitat and species richness in tropical forest remnants. *Biological Conservation* 91: 223–229.
- Gibbs J.P. 1998. Amphibian movements in response to forest edges, roads, and streambeds in southern New England. *Journal of Wildlife Management* 62: 584–589.
- Glaw F. and Vences M. 1994. A Fieldguide to the Amphibians and Reptiles of Madagascar. 2nd edn. Moos Druck, Leverkusen, Germany.
- Goodman S.M., Pidgeon M., Hawkins A.F. and Schulenberg T.S. 1997. The birds of southeastern Madagascar. *Fieldiana Zoology* 87: 1–132.
- Green G.M. and Sussman R.W. 1990. Deforestation history of the eastern rainforests of Madagascar from satellite images. *Science* 248: 212–215.
- Kapos V., Wandelli E., Camargo J.L. and Ganade G. 1997. Edge-related changes in environment and plant responses due to forest fragmentation in central Amazonia. In: Laurance W.F. and Bierregaard R.O. Jr (eds), *Tropical Forest Remnants*. University of Chicago Press, Chicago, Illinois, pp. 33–44.
- Koechlin J. 1972. Flora and vegetation of Madagascar. In: Battistini R. and Richard-Vindard G. (eds), *Biogeography and Ecology in Madagascar*. Junk Publishers, The Hague, The Netherlands, pp. 145–190.
- Laurance W.F. 1999. Introduction and synthesis. *Biological Conservation* 91: 101–107.
- Manly B.F.J. 1997. *Randomization, Bootstrap and Monte Carlo Methods in Biology*. 2nd edn. Chapman & Hall, London.
- Marsh D.M. and Pearman P.B. 1997. Effects of habitat fragmentation on the abundance of two species of Leptodactylid frogs in an Andean montane forest. *Conservation Biology* 11: 1323–1328.
- Matlack G.R. 1993. Microenvironment variation within and among forest edge sites in the eastern United States. *Biological Conservation* 66: 185–194.
- Mesquita R.M., Delamonica P. and Laurance W.F. 1999. Effects of surrounding vegetation on edge-related tree mortality in Amazonian rainforest fragments. *Biological Conservation* 91: 129–134.
- Murcia C. 1995. Edge effects in fragmented forests: implications for conservation. *Trends in Ecology and Evolution* 10: 58–62.
- Pearman P.B. 1997. Correlates of amphibian diversity in an altered landscape of Amazonian Ecuador. *Conservation Biology* 11: 1211–1225.
- Pechmann J.H.K. and Wilbur H.M. 1994. Putting declining amphibian populations into perspective: natural fluctuations and human impacts. *Herpetologica* 50: 65–84.
- Ramanamanjato J.B. 2000. Fragmentation effects on reptile and amphibian diversity in the littoral forest of southeastern Madagascar. In: Rheinwald G. (ed.), *Isolated Vertebrate Communities in the Tropics*. *Bonner Zoologische Monographien* 46. Zoologisches Forschungsinstitut und Museum A. Koenig, Bonn, Germany, pp. 297–308.
- Raxworthy C.J. and Nussbaum R.A. 2000. Extinction and extinction vulnerability of amphibians and reptiles in Madagascar. *Amphibian and Reptile Conservation* 2: 15–23.
- Sartorius S.S., Vitt L.J. and Colli G.R. 1999. Use of naturally and anthropogenically disturbed habitats in Amazonian rainforest by the teiid lizard *Ameiva ameiva*. *Biological Conservation* 90: 91–101.
- Schlaepfer M.A. and Gavin T.A. 2001. Edge effects on lizards and frogs in tropical forest fragments. *Conservation Biology* 15: 1079–1090.
- Stevens S.M. and Husband T.P. 1998. The influence of edge on small mammals: evidence from Brazilian Atlantic forest fragments. *Biological Conservation* 85: 1–8.
- Turton S.M. and Freiburger H.J. 1997. Edge and aspect effects on the microclimate of a small tropical forest remnant on the Atherton Tableland, northeastern Australia. In: Laurance W.F. and Bierregaard R.O. Jr (eds), *Tropical Forest Remnants*. University of Chicago Press, Chicago, Illinois, pp. 45–54.
- Vallan D. 2000. Influence of forest fragmentation on amphibian diversity in the nature reserve of Ambohitantely, highland Madagascar. *Biological Conservation* 96: 31–43.
- Whitmore T.C. 1997. Tropical forest disturbance, disappearance, and species loss. In: Laurance W.F. and Bierregaard R.O. Jr (eds), *Tropical Forest Remnants*. University of Chicago Press, Chicago, Illinois, pp. 3–12.
- Williams-Linera G. 1990. Vegetation structure and environmental conditions of forest edges in Panama. *Journal of Ecology* 78: 356–373.