
Edge Effects on Lizards and Frogs in Tropical Forest Fragments

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Abstract: *We investigated whether forest-pasture edges affect the distribution of an assemblage of small vertebrate ectotherms in a consistent and predictable manner. We describe the abundance and distribution of two species of anoline lizards (Norops) and five species of leaf-litter frogs (Eleutherodactylus) along the edges and in the interiors of nine forest fragments near Las Cruces, Costa Rica. Over 4 months, we surveyed 44 pairs of plots by visual encounter. In each pair of plots, one was immediately adjacent to the pasture and the second was within the forest "interior." Both plots of a pair were searched simultaneously. This block design controlled for the effects of weather, topography, and searcher ability. The distribution of all species was highly variable with respect to edges. Only two species of frogs, Eleutherodactylus podiciferus and E. cruentus, were significantly more abundant in interior plots than in edge plots, although not consistently so. Both species of Norops lizards were more abundant along forest edges during the dry season. Both Norops species and several Eleutherodactylus species, however, appeared to become more abundant in the forest interior after the onset of the wet season, suggesting a seasonal edge effect. In Norops polylepis, the most abundant anole, rates of ectoparasitism were lower along edges than in forest interiors. The magnitude of the edge effect on any one species was not influenced by the size of fragments or by the distance of the interior plot from the nearest edge. We believe that edge effects should not be defined by the distance to which they are detected. Rather, they should be viewed as highly dynamic in space and time; taxa appear to respond to different components of edge effects according to their particular biological requirements.*

Efectos de Borde sobre Lagartijas y Ranas en Fragmentos de Bosque Tropical

Resumen: *Investigamos si los bordes bosque—pastizal afectan la distribución de una comunidad de vertebrados ectotermos pequeños de manera consistente y predecible. Describimos la abundancia y distribución de dos especies de lagartijas anólicas (Norops) y cinco especies de ranas habitantes de la hojarasca (Eleutherodactylus) a lo largo de los bordes y en el interior de nueve fragmentos de bosque cerca de Las Cruces, Costa Rica. Durante cuatro meses utilizamos la técnica de encuentro visual para muestrear 44 pares de parcelas. En cada par de parcelas una estaba adyacente al pastizal y la segunda estaba en el "interior" del bosque. Ambas parcelas de un par fueron muestreadas simultáneamente. Este diseño de bloques controló los efectos meteorológicos, topográficos y de la habilidad del muestreador. La distribución de todas las especies fue altamente variable con respecto a los bordes. Solo dos especies de ranas Eleutherodactylus podiciferus y E. cruentus, fueron significativamente más abundantes en parcelas del interior que en los bordes, aunque esto no fue consistente. Ambas especies de Norops fueron más abundantes a lo largo de los bordes de bosque en la época de sequía. Sin embargo, ambas especies de Norops y varias de Eleutherodactylus aparentemente fueron más abundantes en el interior de los bosques después del inicio de la temporada de lluvias, lo que sugiere un efecto de borde estacional. Las tasas de ectoparasitismo en Norops polylepis, el anólido más abundante, fueron menores en los bordes que en el interior de los bosques. La magnitud del efecto de borde sobre una especie no fue influida por el tamaño de los fragmentos o la distancia de la parcela interior al borde más cercano. Pensamos que los efectos de borde no deben ser definidos por la distancia a la que son detectados. Más bien, deben entenderse como muy dinámicos en espacio y tiempo; los taxones parecen responder a diferentes componentes de los efectos de borde en función de sus requerimientos biológicos particulares.*

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Introduction

Rates of tropical deforestation continue to exceed those of forest regeneration, and edges between forests and surrounding cleared areas are becoming an increasingly ubiquitous feature of tropical landscapes (Whitmore 1997). The term *edge effects* encompasses all the abiotic and biotic changes that arise as a consequence of the juxtaposition of two different habitat types. There is concern that edge effects, some components of which may penetrate deeply into forest fragments, may be detrimental to many native species (e.g., Harris 1988; Yahner 1988; Skole & Tucker 1993; Gascon et al. 2000). The motivation behind our work was to investigate whether the distribution of a small group of amphibian and reptile species showed a consistent pattern between forest edges and forest interiors. Finding a generality in these patterns would help determine whether this group might be adversely affected by the presence of forest-pasture edges.

Murcia (1995) recognized three levels of edge effects: the abiotic changes induced by the presence of an edge, first-order biological changes caused directly by the abiotic changes, and higher-order biological interactions, which are consequences of the first two levels. Abiotic changes known to occur within forest fragments near edges include reduced moisture availability, more extreme temperatures, higher solar radiation, and greater wind disturbance than in forest interiors (Chen et al. 1995; Kapos et al. 1997; Turton & Freiburger 1997). Abiotic changes tend to decline with distance from an edge into a forest, although the steepness of this decline will be a function of the age and aspect of an edge (Kapos et al. 1997; Turton & Freiburger 1997). The consensus is that these abiotic changes generally are not detectable in tropical forests beyond 15–60 m (Laurance et al. 1997), with the possible exception of wind damage, which has been detected several hundred meters from an edge (Laurance 1997). Organisms displaced or favored by the presence of an edge are biotic edge effects. These biotic effects may in turn cause secondary biotic effects such as the alteration of predator-prey and parasite-host relationships. Nevertheless, the importance of spatial and temporal variations in these abiotic and biotic variables remains unclear.

Early models assumed that edge effects penetrated a fixed distance (Laurance 1991; Laurance & Yensen 1991; Malcolm 1994; Ferreira & Laurance 1997). More recent models and field work that have considered the various components of edge effects individually have shown that the distance penetrated by each edge effect varies spatially and temporally with factors such as time of day, season, age of edge, weather, topography, and prevailing winds (Kapos 1989; Chen et al. 1995, 1996; Cadena-so et al. 1997; Kapos et al. 1997; Gascon et al. 2000). Therefore, the area of a fragment that contains the habitat conditions necessary for a given organism to thrive

will not remain static at a predetermined distance from the edge. Instead, suitable conditions may advance, retreat, or even disappear with time (Chen et al. 1996).

Because of their moderate mobility, amphibians and reptiles are ideal organisms for tracking temporally and spatially moderated abiotic edge effects. Amphibians and reptiles are ectotherms, obtaining most of their body heat from their surroundings. Therefore, we expect them to respond behaviorally to temperature changes in their microclimate. Furthermore, amphibians are more prone to desiccation than are reptiles. Because forest edges tend to be sunnier, windier, and drier than forest interiors (Ferreira & Laurance 1997; Kapos et al. 1997), we expect amphibians to be more vulnerable to the presence of an edge than reptiles. Indeed, Pearman (1997) found that the diversity of *Eleutherodactylus* species within a forested fragment increased with distance from edges. Nevertheless, edges can also be beneficial to certain species of amphibians and reptiles if they provide better foraging and reproductive opportunities (Gascon 1993; Pearman 1997) or reduced rates of predation and parasitism.

It is important to understand how amphibians and reptiles respond to a fragmented landscape, given that habitat destruction and fragmentation are leading causes of their world wide decline (Wake 1991; Blaustein et al. 1994b; Sarre et al. 1995). Our objectives were to (1) test whether the abundance of *Norops* lizards and *Eleutherodactylus* frogs differed between edge and interior habitat of tropical forest fragments, (2) to test whether rates of ectoparasitism in *Norops* lizards differed between edge and interior habitat, and (3) to describe the temporal variability of edge effects on the distribution of species across seasons and between day and night. Our results should have broad applicability, because *Eleutherodactylus* and *Norops* (or the closely related genus *Anolis*) are prominent components in the herpetofauna of many Neotropical ecosystems (e.g., Scott 1976; Lieberman 1986; Fauth et al. 1989; Duellman 1993; Lynch & Duellman 1997), where they presumably play an important role ecologically (Reagan 1996; Stewart & Woolbright 1996).

Methods

Study Sites

We conducted our study in nine forest fragments on Fila Cruces (ridge) (lat 8°47'N, long 82°59'W), located near the Las Cruces Biological Station of the Organization for Tropical Studies (OTS) in Coto Brus, Costa Rica. Fila Cruces, described as premontane wet forest (Holdridge 1947 in Hartshorn 1983; L. D. Gómez, personal communication), is within the Costa Rican Biotic Unit 23 (temperate/tropical, very wet, with 1–2 dry months) (Herrera & Gómez 1993). The dry season, which occurs sometime during December–April, is characterized by sunny,

clear skies, strong gusts of wind, and monthly rainfall 10–20% of that of the rainy season (L. D. Gómez, personal communication).

The landscape on Fila Cruces consists of several fragments of primary forest (Fig. 1) created 20–35 years ago (Daily & Ehrlich 1995). Since then all fragments have been continuously surrounded by a matrix of active cattle pastures, with the exception of a small pond between fragments 3 and 4 (Fig. 1). Limited selective logging has probably occurred in some fragments, although records of such activity are unavailable. Further disturbance to the forest fragments caused by cattle is evident along some of the unfenced forest edges.

The region near Las Cruces Biological Station offers an ideal landscape in which to study questions pertaining to edge effects and fragmentation because the fragments have similar logging histories and surrounding matrices, thus controlling for two factors known to influence the magnitude of edge effects. Most fragments on Fila Cruces are <25 ha and close to one another, a pattern typical of other tropical landscapes colonized by humans (Ranta et al. 1998; P. Rich, personal communication). Most fragments <25 ha have been disturbed by wind (Hurricane César, 1996) even near their centers, which suggests that “pristine” forest conditions occur only in the largest fragments. Even if many fragment interiors were not completely free from the influence of edge effects, we assumed that edge effects pertinent to amphibians and reptiles would be much weaker in fragment interiors than along edges.

Study Species

We focused on the leaf-litter herpetofauna, which is dominated by two species of lizards in the genus *Norops* (Iguanidae: Polychrotidae) and five species of leaf-litter frogs in the genus *Eleutherodactylus* (Leptodactylidae).

The *Norops* lizards we encountered were small to medium sized (generally 20–80 mm snout-vent length), semi-arboreal, and diurnal, and they forage primarily for invertebrates in the leaf litter (Andrews 1983). *Norops* reproduce primarily during the rainy season (Andrews 1971; Andrews & Rand 1974). The *Eleutherodactylus* frogs in our study were small (generally 12–25 mm snout-vent length) and terrestrial. All species in our study are presumed to undergo their entire life cycle in the leaf litter: eggs develop directly into small froglets, bypassing the tadpole stage (Townsend & Stewart 1985). These frogs feed primarily on small leaf-litter invertebrates (Lieberman 1986). *Eleutherodactylus* species sampled during this study were all nocturnal, with the exception of *E. podiciferus*, which was captured primarily during the day.

Sampling

To describe the distribution and relative abundance of the herpetofauna, we placed 44 pairs of 10 × 10 m plots across the landscape: one plot in a pair was always located in the forest but within 1–2 m of the edge (“edge” plot), and the other was placed in the “interior” of the same fragment. Interior plots were located near the center of the small (<1 ha) fragments (mean 29 m from the nearest edge; range 13–50 m) and on average 123 m (range 45–330 m) from the closest edge in the medium (9–23 ha) and large (>100 ha) fragments. In placing plots, we avoided stream banks and large, recently-created tree gaps. Each plot within a given pair was located at similar elevation, slope, and aspect. We worked only on “hard” edges, where fencing excluded cattle from forests and where cattle grazing and removal of shrubs prevented secondary succession in the pastures. Within these constraints, we selected plot locations randomly.

We assigned seven plot pairs to each medium and large fragment. Because we were restricted by the small number

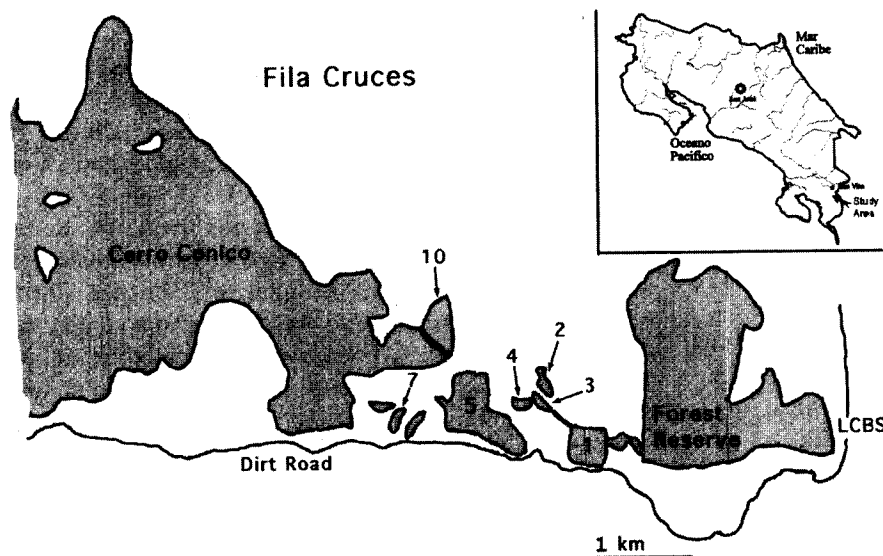


Figure 1. Study site at Fila Cruces, near San Vito, in southern Costa Rica. The forest is shaded, and the nine fragments surveyed are labeled and include Forest Reserve and Cerro Conico. The Las Cruces Biological Station (LCBS) is east of the Forest Reserve. Inset is Costa Rica.

of suitable locations, we could place only one to three plot pairs in each small fragment. Each pair of plots was sampled only once (but included both a day and night search), and the 44 pairs of plots were sampled in random order. The distance from a plot to the fragment's nearest edge ($E1$) was used as a simple indicator of exposure to edge effects.

The study took place from 7 February to 4 June 1997. The dry season began in January, and the transition from dry to wet season occurred abruptly on 18 April. Thus, our study period covered most of the dry season and the first 6 weeks of the wet season. The plots in a pair were surveyed by visual encounter simultaneously by M.A.S. and one field assistant (Crump & Scott 1994) for 90 minutes during the afternoon and again for 90 minutes on the same night. Searchers were randomly assigned a day plot and then switched plots for the night search. Amphibians and lizards up to 2 m above the ground were caught by hand and placed in holding bags for subsequent processing. Animals were identified to species, sexed (when possible), measured (snout-vent length), weighed, toe-clipped, and released at their location of capture. We also counted the number of ectoparasitic chiggers (*Eutrombicula* spp.) in the lizard's dewlap, groin, armpits, and at the base of the tail to estimate rates of parasitism in fragment interiors and edges.

We measured habitat variables within each plot to determine characteristics of interior and edge habitat. We measured elevation, slope, aspect (N, S, W, or E), and diameter at breast height (dbh) of all standing trees that were >7 cm dbh. Trees were subcategorized into buttress trees with aerial support roots, unbuttressed trees, tree ferns, and dead standing trees. For each plot, both searchers independently estimated percent canopy cover throughout the plot at three different heights (0–2, 2–5, +5 m) and indices of leaf-litter volume, vine abundance, and epiphyte and moss load. Indices were scored as follows: none, 0; low, 1; medium, 2; high, 3; very high, 4. Estimates of both searchers were then averaged for each plot. Leaf-litter samples were collected from 50 × 50 cm in the four corners of each plot, placed in zip-lock bags, and taken to the lab, where they were weighed wet. A subsample was weighed wet, dried for 24 hours at 65° C, and then weighed to yield percent moisture content and a measure of dry leaf biomass per square meter. We excluded measures of leaf-litter moisture if it rained between the collection of the leaf litter samples from the two plots.

Analyses

We analyzed the effects of edges on the abundance of each species by considering the net difference between counts in the two plots within a pair ($n_{\text{interior}} - n_{\text{edge}}$, or $I - E$). Because plots within a pair were similar with respect to elevation, slope, aspect, weather, and searchers, except for the presence or absence of an edge, the

value of $I - E$ should reflect the effect of the edge on a species' abundance. To analyze $I - E$ statistically across all 44 pairs, we applied the Wilcoxon paired-sample signed-ranks (PSSR) test (Conover 1999) to the pairs of raw counts (I and E). Although the pairs of plots from within the same fragment are less independent statistically of one another than are pairs of plots from different fragments, we assumed that all pairs are equally independent of one another biologically given the proximity of the different fragments to one another. We were interested primarily in testing for an edge effect, not in a fragment-area effect, but we included pairs of plots from various fragments to increase our sample sizes and our statistical universe. We used Spearman's r_{bo} to test for an association between the magnitude of $I - E$ and the distance from the interior plot to the nearest edge ($E1$), and we used Mood's median to test for differences in $I - E$ between the different fragment-size categories (small, medium, large). Wilcoxon PSSR tests were used to test for differences in habitat measures between interior and edge plots. Seasonal changes of abundance were described in a post-hoc manner, based on locally weighted regression scatterplot smoothing (LOWESS) nonparametric regression lines (0.8 smoothing, 2 steps) (Trexler & Travis 1993).

We analyzed parasite loads on *N. polylepsis* and *N. woodi* with a general linear model (GLM). Predictor variables included sex of the lizard, fragment identity, fragment category (small, medium, large), plot type (interior or edge), and Julian date. Snout-vent length (SVL) was entered as a covariate. The response variable—total number of ectoparasites counted on each lizard—was log-transformed to satisfy the assumptions of the GLM.

Results

Overall, we captured 784 individuals of 18 species (Appendix). Most individuals captured were either leaf-litter frogs in the genus *Eleutherodactylus* (69% of total) or anoline lizards in the genus *Norops* (28% of total). We encountered at least 1 *Eleutherodactylus* frog in 97% (85 of 88) of all plots, and ≥1 *Norops* lizard in 78% (69 of 88) of all plots. We captured a mean of 3.70 (SD = 1.84) species of lizards and frogs in edge plots and a similar mean of 3.75 (SD = 1.60) species in interior plots. Juveniles from both genera could not always be identified reliably to species ($n = 51$; 6% of total) and were excluded from species-specific analyses. We had fewer than 15 total captures of 11 species of frogs, toads, lizards, or salamanders (Appendix), and these were not included in the species-specific analyses because of low sample size. Only 4 (0.7%) *Eleutherodactylus* individuals and 9 (4.1%) *Norops* individuals were recaptured at night after being marked in the same plot during the afternoon search, but none moved among plots. Recaptures were not counted.

Lizards (*Norops*)

We captured about 50% more *N. polylepis* individuals in edge plots than in interior plots (Table 1). Blocking by paired sample, *N. polylepis* was significantly more abundant along edge plots than in interior plots (Wilcoxon PSSR, $T^+ = 171.0$, $p = 0.031$; Table 2). Also, *N. woodi* were more abundant in edge plots than in interior plots (mean 1.32 vs. 0.86 respectively; Table 1), but this difference was not significant when blocked by paired sample (Wilcoxon PSSR, $T^+ = 105.0$, $p = 0.075$; Table 2).

Both species showed a similar seasonal pattern: they were more abundant along edges during the dry season and appeared to become more abundant in the forest interior with the onset of the wet season (Fig. 2). Around this apparent seasonal trend, however, there was considerable variation in each species' response to edges from site to site (or day to day): values of $I - E$ for *N. polylepis* ranged throughout the study area from -6 to $+6$ (Fig. 2a), and values of $I - E$ for *N. woodi* ranged from -5 to $+3$ (Fig. 2b). We were unable to detect a significant influence of fragment size (small, medium, large) or the distance from interior plot to the nearest edge (E1) on the value of $I - E$ for either *Norops* species (Table 2; Fig. 2).

In *N. polylepis*, 72 of 119 individuals (61%) had ≥ 1 ectoparasite. The number of mites per *N. polylepis* lizard increased significantly with size of the lizard ($F_{1,116} = 74.7$, $p < 0.001$). There were significantly more mites on lizards caught in interior plots than on those caught in edge plots when SVL was entered as a covariate ($F_{1,116} = 10.6$, $p = 0.001$; the SVL \times plot type interaction was not significant). Sex, date, and fragment identity did not explain a significant amount of the remaining variation when added individually to the model. The regression line for *N. polylepis* versus log-parasites was $\ln(\text{parasites} + 1) = -1.42 + 0.0662 \times \text{SVL}(\text{mm})$ ($r^2 = 0.40$) and $\ln(\text{parasites} + 1) = -1.14 + 0.0478 \times \text{SVL}(\text{mm})$ ($r^2 = 0.36$) for interior and edge plots, respectively. In other words, an adult lizard (50 mm SVL) had on average twice as many mites if captured in an interior plot (5.6) than in an edge plot (2.5).

In *N. woodi*, 61 of 95 individuals (64%) had ≥ 1 parasite. The number of ectoparasites per lizard increased with the size of the lizard ($F_{1,94} = 35.0$, $p < 0.001$) and with date of capture ($F_{1,94} = 8.1$, $p < 0.006$). The number of ectoparasites per *N. woodi* lizard also differed significantly between individual fragments ($F_{6,94} = 2.4$, $p = 0.035$) when SVL and date were entered as covariates. Pair-wise comparisons (adjusted for multiple comparisons) showed no significant differences between fragments, suggesting a complex pattern. As in *N. polylepis*, there were more ectoparasites on *N. woodi* lizards caught in interior plots than on those caught in edge plots (0.96 vs. 0.74; log values), although the difference was not significant when entered into the model with SVL, date, and fragments ($p = 0.17$). Sex did not explain a significant amount of the remaining variation.

Leaf-Litter Frogs (*Eleutherodactylus*)

Eleutherodactylus podiciferus, the only frog species active during the day, and *E. cruentus* were significantly more abundant in interior plots than in edge plots (Wilcoxon PSSR, $T^+ = 568.5$, $p < 0.001$, and $T^+ = 107.0$, $p = 0.047$, respectively) (Table 2; Fig. 3). For both of these species, there were approximately two or three times as many individuals on average in interior plots than in edge plots (Table 1). The other three species of *Eleutherodactylus* were not more abundant statistically in either interior or edge plots (Wilcoxon PSSR, $p > 0.05$; for all three species) (Table 2; Fig. 4), although *E. stejnegerianus* was more than twice as abundant in interior plots than in edge plots (Table 1). All species showed considerable variation in their relative abundance along edges ($I - E$) from plot pair to plot pair. Even *E. podiciferus*, the most consistently edge-phobic of the species studied, was occasionally more abundant in the edge plots (Fig. 3a) and had $I - E$ values that ranged from -4 to $+13$.

We were unable to detect a significant influence of fragment size (small, medium, large) or distance from the interior plot to the nearest edge (E1) on the value of $I - E$

Table 1. Median (range) and mean (SD) of counts of amphibians and reptiles captured in interior and edge plots in Fila Cruces, Costa Rica, February–June 1997.

Species	Interior		Edge	
	median (range)	mean (SD)	median (range)	mean (SD)
Lizards				
<i>Norops polylepis</i>	0.5 (0–6)	1.05 (1.38)	1 (0–7)	1.66 (1.72)
<i>N. woodi</i>	1 (0–4)	0.86 (1.17)	1 (0–7)	1.32 (1.76)
Frogs				
<i>Eleutherodactylus cruentus</i>	0 (0–9)	0.64 (1.49)	0 (0–3)	0.18 (0.54)
<i>E. podiciferus</i>	2 (0–14)	2.93 (3.13)	1 (0–7)	1.11 (1.58)
<i>E. ridens</i>	1 (0–14)	2.11 (2.71)	1 (0–9)	1.95 (2.40)
<i>E. stejnegerianus</i>	0 (0–7)	0.48 (1.21)	0 (0–2)	0.16 (0.43)
<i>E. vocator</i>	0 (0–6)	0.50 (1.13)	0 (0–5)	0.70 (0.17)
Sampling efforts (plots searched)	44		44	

Table 2. Results of tests for the presence of an edge effect^a on several frog and lizard species and on whether the magnitude of the edge effect is correlated with distance to the nearest edge (E1) and fragment size in Fila Cruces, Costa Rica.

Hypothesis ^a	Statistical test ^b	N. polylepis	N. woodi	E. cruentus	E. podiciferus	E. ridens	E. stejnegerianus	E. vocator
Species is equally abundant along edge and interior plots $H_0: I - E = 0$	Wilcoxon's paired-sample signed-rank test ^c	$n = 38$ n for test = 34 $T^{++} = 171.0$ median = -1.0 $p = 0.031$	$n = 28$ n for test = 26 $T^{++} = 105.0$ median = -1.0 $p = 0.075$	$n = 17$ n for test = 16 $T^{++} = 107.0$ median = 1 $p = 0.047$	$n = 39$ n for test = 36 $T^{++} = 568.5$ median = 1.5 $p = < 0.001$	$n = 36$ n for test = 31 $T^{++} = 265.0$ median = 0.0 $p = 0.746$	$n = 14$ n for test = 11 $T^{++} = 51.0$ median = 1.0 $p = 0.120$	$n = 23$ n for test = 21 $T^{++} = 86.5$ median = -0.5 $p = 0.322$
Magnitude of $I - E$ is independent of the distance from the nearest edge (E1) H_0 : nonsignificant association between the rank of $I - E$ and the rank of distance to E1	Spearman's rho ^d	$n = 38$ $\rho = -0.093$ $p > 0.1$	$n = 28$ $\rho = 0.141$ $p > 0.1$	$n = 17$ $\rho = 0.189$ $p > 0.1$	$n = 39$ $\rho = -0.218$ $p > 0.1$	$n = 36$ $\rho = 0.026$ $p > 0.1$	$n = 14$ $\rho = 0.47$ $p > 0.1$	$n = 23$ $\rho = 0.232$ $p > 0.1$
Magnitude of $I - E$ does not vary between fragments of different sizes H_0 : ranks of $I - E$ do not differ significantly between fragment-size categories ^f	Mood's median test ^e	$\chi^2 = 1.26$ df = 2 $p = 0.534$	$\chi^2 = 3.19$ df = 2 $p = 0.203$	$\chi^2 = 0.5$ df = 2 $p = 0.778$	$\chi^2 = 5.4$ df = 2 $p = 0.065$	$\chi^2 = 1.55$ df = 2 $p = 0.460$	$\chi^2 = 1.12$ df = 2 $p = 0.571$	$\chi^2 = 0.48$ df = 2 $p = 0.785$

^aEdge effect is defined as the difference in abundance between interior (I) and edge (E) plots.

^bAll tests are two-sided with significance at $p = 0.05$.

^cTies are excluded, reducing the sample size.

^dSignificance was tested by comparing ρ to w , where $w = z/(\sqrt{n - 1})^{1/2}$ and where z is the standard normal quantile (Conover 1999).

^eMood's median test is less susceptible to outliers than Kruskal-Wallis (Conover 1999).

^fFragments were grouped into three categories (small, <1 ha; medium, 9-27 ha; large, >100 ha) to ensure a sufficiently large sample size for each size factor.

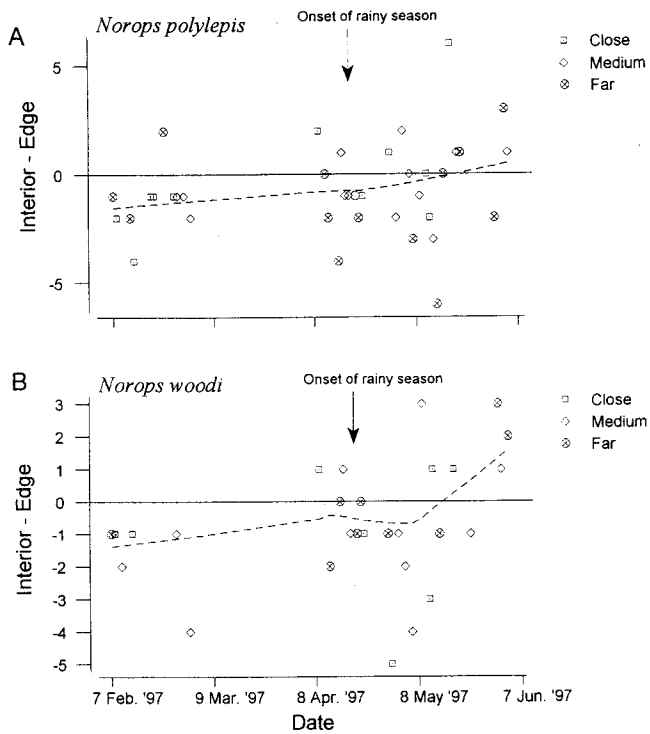


Figure 2. Effect of edges on (a) *Norops polylepis* ($n = 38$ pairs of plots) and (b) *Norops woodi* ($n = 28$ pairs of plots) in Fila Cruces, Costa Rica. Each point represents the difference between the interior and edge (interior-edge) plot from one pair. Points above zero therefore represent pairs of plots for which there were more individuals in the interior plot than in the edge plot. The dashed line is a LOWESS regression. Three symbols are used to indicate how far the interior plot was from the nearest edge (E1): <50 m, close; 51–100 m, medium; and >100 m, far. Note the different scales.

for any of the *Eleutherodactylus* species (Table 2; Figs. 3 & 4). Finally, the three *Eleutherodactylus* species for which we could not detect significant differences in abundance between edge and interior plots (*E. stejnegerianus*, *E. ridens*, and *E. vocator*) appeared to become progressively more abundant in the interior plots after the onset of the rainy season (Fig. 4).

Habitat Characteristics within Interior and Edge Plots

We detected significant differences between interior and edge plots in six habitat variables (when blocked by paired plots to control for the effects of elevation, topography, slope, and aspect). Interior plots had significantly denser overstories (+5 m), sparser understories (0–2 m, 2–5 m), more buttress trees (both in numbers and basal area), and fewer vines than edge plots (Table 3). We did not detect a difference in elevation and slope between edge and interior plots (Wilcoxon's signed rank test, $p > 0.2$ for both variables; Table 3), suggesting that these fac-

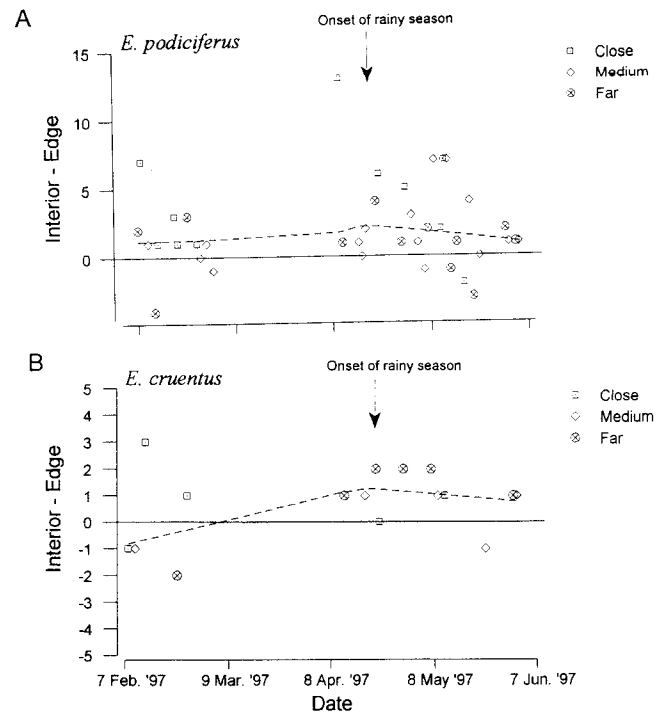


Figure 3. Effect of edges on (a) *Eleutherodactylus podiciferus* and (b) *E. cruentus* in Fila Cruces, Costa Rica. Each point represents the difference between an interior and edge plot (interior-edge) ($n = 39$ pairs of plots for *E. podiciferus*; $n = 17$ for *E. cruentus*). Points above zero are from pairs of plots where there were more individuals in the interior plot than in the edge plot. Both species were on average significantly more abundant in interior plots. Note the different scales. Definitions for key as in Fig. 2.

tors were adequately controlled for by our paired-plot design. About half (48%) of the pairs of plots had the same aspect, 22 (50%) were offset by 90° , and only one pair (2%) had opposite aspects. There was no detectable difference between edge and interior plots in dry leaf-litter mass and percent leaf-litter water content, even when this test was restricted to data from the dry season (Table 3).

Discussion

General Trends

The purpose of our study was to investigate whether a group of lizard and frog species showed a consistent response to the presence of edges. Although some species were significantly more abundant in edge plots (*Norops polylepis*) and others in interior plots (*E. podiciferus* and *E. cruentus*), the high variation in species' responses to edges was unexpected. The cause for this high variation may be the unlimited number of possible combinations of all the abiotic and biotic components and all their

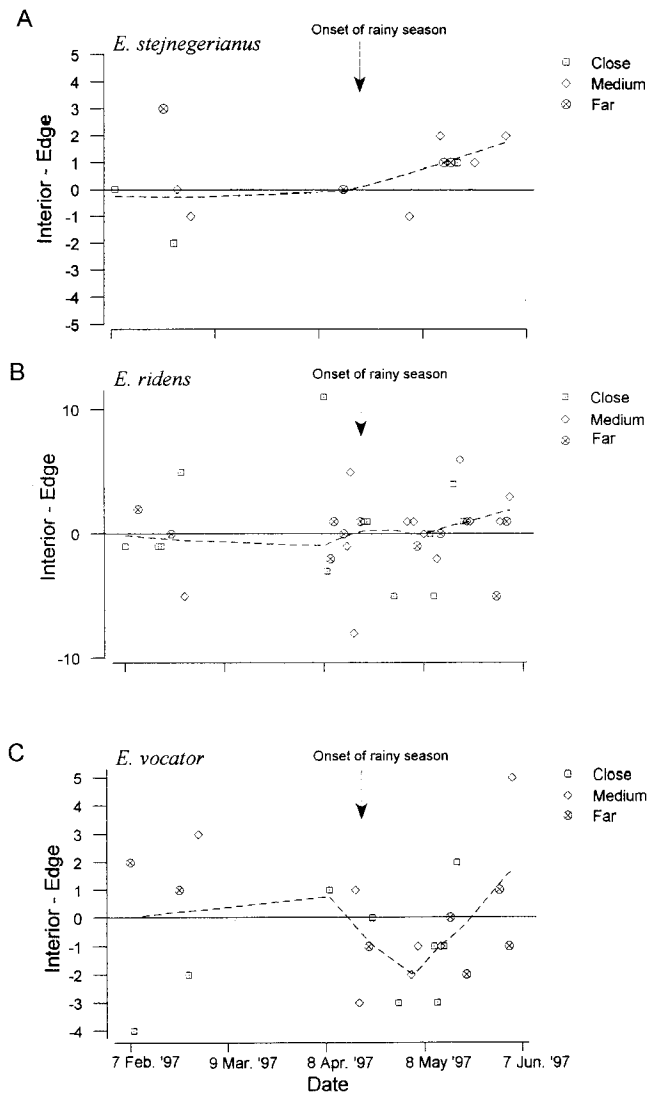


Figure 4. Effect of edges on (a) *Eleutherodactylus stejnegerianus*, (b) *E. ridens*, and (c) *E. vocator* in *Fila Cruces*, Costa Rica. Each point represents the difference between an interior and edge plot (interior-edge) ($n = 14$ pairs of plots for *E. stejnegerianus*; $n = 36$ for *E. ridens*; $n = 23$ for *E. vocator*). All three species were on average equally abundant in interior and edge plots. Note the different scales. Definitions for key as in Fig. 2.

possible interactions that make up an “edge effect.” Each species presumably is adapted to a unique set of ecological conditions. Any given set of conditions is unlikely to be consistently found (or absent) along edge habitat, because the manner in which each component varies as a function of distance from an edge is likely to be affected by topography, elevation, slope, aspect, history of the site, and abiotic and biotic components.

We sampled a relatively restricted subset of edge types—only hard edges between pasture and forests,

fenced, same age, no streams, in one small region—and attempted to control for the effects of elevation, slope, and aspect. Sampling a wider range of edge-types would probably yield an even greater amount of variation in the responses of each species. We suspect that broad, predictable responses to edges may be difficult to obtain for any taxon and that a better understanding of each species’ autecology will be necessary to predict the effect of forest-pasture edges on frogs and lizards.

Edges and Lizards

The *Norops* lizard species showed much variation in their response to edges, although both species displayed a similar pattern overall. Both *N. polylepis* and *N. woodi* were generally more abundant in edge plots during the end of the dry season. After the onset of the rainy season, both species appeared to become more abundant in interior plots than in edge plots (Fig. 2). We found only one study that reported examples of biotic seasonal edge effects in the tropics. Restrepo and Gómez (1998) found that the abundance of frugivorous and insectivorous birds along forest edges in montane Colombia differed between dry and wet seasons. Given that most tropical landscapes experience climates with important seasonal differences in rainfall, sunlight, temperature, and wind, we suspect that seasonal differences in edge effects may be common.

There were significantly fewer parasites on *N. polylepis* caught in edge plots than in interior plots, and a similar trend was observed for *N. woodi*. This result can be explained by the fact that *Eutrombicula* mites tend to favor cool, shady, and moist habitat over sunny and dry habitat (Zippel et al. 1996). Parasitism always carries a fitness cost (Keymer & Read 1991), although it remains to be demonstrated that this cost is significant in a *Norops*-*Eutrombicula* association.

We speculate that *Norops* lizards may migrate toward forest edges during the dry season, when they are non-territorial and not reproducing (Andrews 1971). Edge habitat may provide benefits such as higher insect abundances (Didham 1997 and references therein) and reduced rates of parasitism (this study) or predation relative to forest interiors. With the onset of the rains, *Norops* males and females become territorial and spend a significant portion of their time courting or defending their territories (Andrews & Rand 1974; Fleming & Hooker 1975). *Norops* may return to forest interiors during the wet season if interior habitat provides some reproductive advantage, such as reduced predation, reduced competition for territories, and increased egg survival. Future studies may reveal that species exploit edge and interior habitats selectively depending on time of day, weather conditions, seasons, or life stage (Noss 1991; Restrepo & Gómez 1998).

Table 3. Comparison of habitat variables between the 44 interior (I) and edge (E) plots in Fila Cruces, Costa Rica, by Wilcoxon paired-sample signed-rank test (T^+).

Habitat variable	Interior median (range)	Edge median (range)	n test ^a	Median (I - E)	T^+	p
Elevation (m)	1291 (1170-1400)	1294(1198-1390)	39	-2.5	298.0	0.202
Slope (°)	26 (5-47)	28.5 (6-42)	43	-0.5	430.0	0.608
Total trees	14 (6-26)	15 (6-32)	41	-1	381.5	0.550
Total diameter at breast height (dbh) (cm)	229 (99-382)	227 (111-441)	44	-8	435.0	0.651
Dead trees	0 (0-2)	1 (0-2)	26	0	166.0	0.819
Dead tree dbh (cm)	0 (0-129)	16 (0-145)	29	-10	165.0	0.261
Buttress trees	2 (0-5)	1 (0-8)	28	1	338.0	0.002
Buttress tree dbh (cm)	53 (0-134)	15 (0-113)	36	22	520.0	0.003
Unbuttressed trees	7.5 (0-17)	9.5 (1-22)	44	-1	372.0	0.225
Unbuttressed tree dbh (cm)	142 (0-382)	148 (10-426)	44	-13	395.0	0.349
Tree ferns	3 (0-13)	3 (0-22)	38	-0.5	307.5	0.365
Tree fern dbh (cm)	34 (0-129)	36 (0-201)	41	-11	321.0	0.158
Canopy cover 0-2 m (÷)	50 (15-80)	65 (20-90)	40	-10	238.0	0.021
Canopy cover 2-5 m (÷)	35 (10-75)	45 (15-75)	42	-12.5	196.0	0.001
Canopy cover 5+ m (÷)	80 (35-95)	65 (15-90)	42	15	792.0	0.001
Leaf index	2 (1-3)	2 (1-3)	31	0	263.5	0.769
Vine index	2 (0-3)	2 (0-4)	35	-0.5	128.5	0.002
Epiphyte index	2 (0-3)	2 (0-3)	26	0	213.0	0.347
Dry leaf mass (g/m ²)	216 (115-426)	193 (98-416)	42	12	536.5	0.291 ^b
Leaf moisture (%)	274 (35-455)	255 (33-428)	42	1	495.0	0.591 ^b

^aThe n test may be smaller than n = 44 because ties were removed.

^bThese variables did not differ significantly even when only the dry-season data were considered.

Edges and Frogs

Eleutherodactylus podiciferus and *E. cruentus* were significantly less abundant in edge plots than in interior plots (Table 2; Fig. 3; & Appendix 1). In general, species negatively affected by edges run a higher risk of local extirpation in a fragmented landscape. For example, if a large band of habitat around the edge of a fragment is not suitable to a species, its population numbers may be relatively depressed in small fragments (Yahner 1988). Furthermore, negative edge effects may reduce the probability of dispersal between fragments. Consequently, a population could be subject to greater risks of extirpation from stochastic environmental, genetic, and demographic events (Saunders et al. 1991).

Why *E. podiciferus* and *E. cruentus* are less abundant in edge plots is not clear. A number of possible explanations exist, including predation and prey abundance, but here we discuss the possible role of two factors for which we have some data: habitat characteristics and abiotic factors. Certain habitat characteristics associated with edge plots (Table 3) may not be favorable to these species. For example, we observed that *E. podiciferus* occasionally take refuge between the roots of buttress trees. It may be that the lower abundance of buttress trees along forest edges reduces the abundance of *E. podiciferus*.

The abiotic conditions generally associated with edges—dry, sunny, warm—may have also excluded either of these two species from the edges. This explanation is most likely to apply to the diurnal *E. podiciferus*, be-

cause abiotic edge effects are more pronounced during the day. At night the abiotic differences between pasture and forest are largely obscured (M. A. Schlaepfer, unpublished data). Working in some of the same fragments as we did, Daily and Ehrlich (1996) found that (nocturnal) moth species were more evenly distributed across forest patches and pastures than (diurnal) butterfly species, which were often absent from pastures and small fragments. Daily and Ehrlich (1996) suggest that nocturnal, abiotic conditions are relatively homogeneous across the landscape, facilitating movement of nocturnal organisms between patches. Many of the factors that could be excluding frogs from edge habitat, such as high temperatures, reduced air humidity, reduced leaf-litter humidity (Kapos 1989), or increased UV-B radiation (Blaustein et al. 1994a), are probably moderated at night. We speculate that diurnal amphibians may be particularly vulnerable to edge effects in many tropical landscapes given that edges generally present abiotic conditions (sunny, dry) during the day that are unfavorable to the physiological needs of amphibians (cool, moist).

We acknowledge the possibility that differences in habitat between interior and edge plots (Table 3) may have caused a search bias for which we could not control. For example, the denser understory vegetation (0-2 m) in edge plots could have conceivably caused us to overlook (on the leaf litter) a larger proportion of *E. podiciferus* individuals than in the more open interior plots. We deliberately chose a long search time per plot (two searches of 90 minutes each) to ensure that even the densest plots would be searched thoroughly. Even if such a bias

did exist, we believe that it could not explain the almost three-fold greater overall abundance of *E. podiciferus* in interior plots relative to edges (Table 1). All other species, which were generally encountered on tree trunks or on exposed leaves, were less prone to this bias.

The remaining nocturnal *Eleutherodactylus* frogs were distributed more equally across edge and interior habitat (e.g., Fig. 4), but these species appear to become progressively more abundant in the interior plots after the onset of the rainy season. As with the *Norops* lizards, these data suggest a seasonal edge effect. The direction of this seasonal trend, if confirmed, is a surprising one. We would have expected the desiccation-prone amphibians to avoid edges during the dry season and then move toward the edge with the onset of the rainy season. Future studies could investigate the alternative mechanisms, including prey abundance, predation, and reproductive success in different habitats, that might be driving such a pattern.

Conclusions

The higher abundance of *Norops* lizards along forest edges suggests that *Norops* may benefit from this habitat, at least during part of the year. If this is the case, habitat fragmentation and edge effects may actually be bolstering the number of *N. polylepis* and *N. woodi* in this landscape relative to the forest area available. But despite higher abundances, edges may represent a population sink if survival there is lower (Van Horne 1983; Pulliam 1988). We are currently conducting egg survival experiments and long-term mark-recapture studies along edge gradients to address the question of survival and reproductive success in this relatively novel habitat.

Species-specific responses to edges were apparent among all *Eleutherodactylus* species in this study (Figs. 3 & 4). Pearman (1997) and Marsh and Pearman (1997) also found that *Eleutherodactylus* frogs showed species-specific responses to edges in Ecuador, as did Gascon (1993) with frogs in central Amazon. An important implication for conservation biologists is that even in *Eleutherodactylus*, the most speciose vertebrate genus in the world (Lynch & Duellman 1997), species presumably exploit unique combinations of ecological conditions and play distinct ecological roles; they are not interchangeable.

The distance into a fragment to which edge effects are detectable is likely to change over space and time. Edge effects should be viewed as dynamic, and studies of edge effects should cover several temporal and spatial scales to integrate their full effect. Amphibians and reptiles, with their contrasting physiological and ecological requirements, are useful organisms for tracking spatial and temporal edge effects. Frogs and lizards do not respond uniformly to edges because the effects of edges are many and each species' requirements will interact with these factors in a different manner.

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Appendix

Abundance of all amphibian and lizard species encountered in Fila Cruces, Costa Rica, February–June 1997, by fragment and habitat.^a

Species	Fragments ^b								
	small				medium			large	
	2	3	4	7	1	5	10	CC	FR
I/E	I/E	I/E	I/E	I/E	I/E	I/E	I/E	I/E	I/E
Frogs and toads									
<i>Bufo coniferus</i>	1/—	—/—	—/—	—/—	—/—	—/—	—/—	—/—	—/—
<i>Eleutherodactylus crassidigitus</i>	—/—	—/—	—/—	—/—	—/—	—/1	4/—	1/1	1/1
<i>E. cruentus</i>	2/—	—/1	4/1	—/—	2/3	5/2	11/—	3/1	1/—
<i>E. melanostictus</i>	—/—	—/—	—/—	—/—	—/—	—/1	—/—	—/—	—/—
<i>E. pardalis</i>	—/—	—/—	—/—	—/—	—/—	1/—	—/1	—/1	—/—
<i>E. podiciferus</i>	5/2	30/3	15/8	3/—	12/4	28/18	21/5	11/4	4/5
<i>E. ridens</i>	22/6	6/15	2/1	—/1	15/10	7/22	22/13	7/9	12/9
<i>E. stejnegerianus</i>	—/2	1/1	—/—	—/—	4/1	1/—	2/—	3/2	10/1
<i>E. vocator</i>	1/3	—/7	1/1	—/—	3/2	4/10	10/2	—/2	3/4
<i>Hyla ebraccata</i>	—/—	—/—	—/—	—/—	—/—	—/—	—/—	—/—	—/1
<i>Smilisca phaeota</i>	—/—	—/—	—/—	—/—	—/—	—/—	—/1	—/—	—/—
Lizards									
<i>Norops capito</i>	1/1	—/—	—/—	—/—	—/—	—/—	—/1	—/1	—/3
<i>N. polylepis</i>	3/2	1/5	—/5	—/1	17/8	2/9	7/13	2/3	14/27
<i>N. sp. 1^d</i>	—/—	—/—	—/—	—/—	—/—	—/—	1/—	—/—	—/—
<i>N. sp. 2^d</i>	—/—	—/—	—/—	—/—	—/—	—/—	—/—	—/—	—/1
<i>N. woodi</i>	3/5	4/4	1/3	—/—	14/15	10/14	—/—	4/10	2/7
<i>PtychoGLOSSUS plicatus</i>	1/1	—/1	—/—	—/—	1/1	1/—	1/—	1/—	1/3
Salamanders									
<i>Oedipina</i> complex	—/—	—/—	—/—	—/1	2/—	—/1	1/—	1/—	—/1
Sampling efforts (pairs of plots)	3	3	2	1	7	7	7	7	7

^aUncertain identifications were excluded.^bI, interior; E, edge plot; CC, Cerro Conico; FR, forest reserve.^cOn-line photographs at www.dnr.cornell.edu/edge^d*Norops sp. 1* (University of Costa Rica collection #13249) and *N. sp. 2* (vertebrate collection, Cornell University #13295) remain unidentified.