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EDGE EFFECTS IN SEED AND EGG PREDATION AT TWO NEOTROPICAL RAINFOREST SITES

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Abstract

Depredation of seeds and eggs in a Belizian rainforest was investigated using peanuts and hen's eggs. Seed predation rates were significantly higher 500 m into the forest from the edge than 30 m and 100 m from the edge. Conversely, egg predation was higher in a 100 m zone near the edge. These edge effects were evident even though the edge was a minor road through otherwise continuous forest. In a similar study, in Veracruz, Mexico, using seeds of the canopy tree Brosimum alicastrum, *seed predation followed a similar trend to that observed in Belize. Having accounted for the variation in seed production between trees, the level of predation on* Brosimum *seeds increased with the distance from the forest edge.*

The effects of habitat edges on seed and egg predators have potential implications for their dynamics in fragmented landscapes. It is speculated that when an edge is created where previously there was continuous, pristine forest, edge effects may affect the community structure through their impact on the recruitment of plants and egg-laying animals.

Key words: Mexico, Belize, *Brosinium alicastrum*, mammals, edge effects, seed predation.

INTRODUCTION

Habitat fragmentation increases the edge/forest-interior ratio (Ranney *et al.*, 1981). Biodiversity conservation in the increasingly fragmented natural habitats worldwide requires an understanding of the effects of habitat edges on community dynamics.

Some animals, notably forest interior birds, are known to be scarce near habitat edges (Whitcomb *et al.*, 1977, 1981; Gates & Gysel, 1978; Lovejoy *et al.*, 1986; Andrén, 1992). Others thrive in disturbed areas, early successional, and transitional zones (Bider, 1968; Diamond, 1976; Robbins, 1980; Whitcomb *et al.*, 1981; Brittingham & Temple, 1983; Kroodsma, 1984). Studying animal movements and habitat selection often involves laborious tracking, trapping and radio-tagging. The distribution of seed- and egg-predators, however, can be studied indirectly through their effect on the food they eat. Seed- and egg-predators are especially interesting from a conservation perspective because their activities can have consequences on seedling establishment and on bird reproductive success (e.g. Skutch, 1985; Wilcove, 1985; Sork, 1987). The questions I address here are: Do seed and egg predators shun or prefer forest edges? More specifically, does seed and egg predation increase or decrease with increasing distance from the edge? The answers to these questions can provide a better understanding of the possible fate of species inhabiting subdivided landscapes and of how edge effects can impose limits on the utility of corridors between reserve fragments. Knowledge about the effect of edges on seed and egg predation may influence decisions about reserve design.

I investigated edge effects on seed and egg predation in Rio Bravo, Belize (17°45' N, 89° W) and, on seed predation only, at Los Tuxtlas Biological Station in Veracruz, Mexico (18° 30' N, 95° 04' W). Nomenclature of plants follows Ibarra Manríques and Sinaca Colín (1987) and that of mammals Hall (1981) and Emmons (1990).

METHODS

Rio Bravo, Belize

The Rio Bravo preserve is located in north-western Belize, near the Mexican and Guatemalan borders. The forest at Rio Bravo is medium high and little-disturbed subtropical moist forest, subject to chicle-tapping and selective logging until the 1960s (Brokaw & Mallory, 1988).

A straight 250-m stretch of gravel road, through otherwise continuous forest, with moderate traffic (3–4 vehicles per day), was selected to serve as forest edge. A 10-m strip with grasses and herbaceous vegetation separated the road from the forest edge. Three transects were established parallel to the road at 30, 100 and 500 m from the edge. Along each of these transects 25 cardboard squares (10 × 10 cm) were distributed at 10-m intervals, and five shelled peanuts placed on each square. Fifteen hen's eggs were also placed at regular intervals along each transect. The use of 'exotic' seeds (and eggs) ensures that the predators are not specialists with idiosyncratic behaviors that would prohibit generalization.

Paths were not cleared along the transects and every effort was made to minimize the impact of setting up

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the experiment. Eggs and seeds were checked after two days. Seeds were replaced, moved a few meters, and checked a second time after two more days, giving a total sample size of 50 sites on each transect. There was no association in the fates of seeds between adjacent sites. The cardboard trays were often crawling with minute reddish brown ants (probably *Pheidole* sp.) that nibbled at the peanuts—sometimes a nut was almost completely eaten by ants. To estimate relative seed removal by animals other than ants, 'two or more peanuts removed' vs 'no peanuts removed' was used as the test statistic. This effectively corrected for ant removal because ants nibble slowly and rarely ate a whole peanut. In addition, the statistic 'one or more peanuts removed' was used where few or no ants were present. Using 'removal' vs 'non removal' of seeds as the test statistic also removes the biases resulting from non-independence of peanuts within a cardboard tray.

Levels of seed and egg predation at different distances from the edge were compared using χ^2-values from contingency tables.

Veracruz, Mexico

The Los Tuxtlas region of Veracruz State contains the northernmost tropical rainforest in the Neotropics (Dirzo & Miranda, 1991), and experiences a pronounced dry season from March to May. This study was carried out in June and July 1991. On one side of the forest tract the edge was a dirt road with moderate traffic (2–10 vehicles per day), on the other an area cleared for cattle grazing. The vegetation is characterized as 'high evergreen rainforest' (Dirzo, 1987). Beside *Astrocaryum mexicanum*, *Brosimum alicastrum* was the most important fruiting tree at the time of investigation. *Pseudolmedia oxyphillaria, Dussia mexicana, Guarea glabra, Clarissia biflora* (rare), *Nectandra biflora* (uncommon), *Pitecelobium arboreum*, and *Cymbopetalum baillonii* were also producing some fruit at the time, but this 'background seed source' appeared insignificant.

Fourteen fruiting females of *Brosimum alicastrum* were selected where they could all be sampled in one day. The distance from each tree to the forest edge, which ranged from 30 to 240 m, was measured with a 30-m Leitz fiberglass measuring tape. Seeds were collected from a tree outside the sampling area and checked for endoparasites, then sewed onto a 2-m piece of fishing line. The seeds were pierced once with a needle, the fishing line pulled through and a knot made on the far side. Seeds could be detached with a light tug, and the treatment did not appear to affect germination success or the external characteristics of the seeds. The other end of the fishing line was attached to a sapling or other conveniently positioned object (marked with a 2–3 cm piece of red tape) on arcs around each tree. Two seeds were placed approximately 1 m from opposite sides of the trunk. Five seeds were placed on each of five arcs at 5, 10, 15, 20 and 25 m from the trunk, for a total of 27 seeds per tree. By placing seeds on arcs (as opposed to complete circles), they could be directed away from the nearest neighboring *Brosimum* tree. Adjacent seeds were 5 m apart, enough to ensure independence (Eugene Schupp, pers. comm.). The status (gone, untouched, eaten, entry-exit hole, parasitized, rotten, viable/inviable, nibbled, root-sprout broken/dead, and germination status) of each seed was determined after three weeks. Frequently seed remnants were found near the fishing line and tooth marks identified on the end of the line, suggesting that removed seeds were actually consumed by the predator.

At 45 sites along the same arcs all naturally occurring seeds were counted within a 25 × 25 cm wooden frame. Sampling squares were placed 1 m from where the fishing line was attached, on the straight line towards the adjacent seed attachment on the same arc (in both directions). The sites on each end of the arc had only one sampling square, towards the other sites. On the inner arc sampling squares were placed 1 m from the trunk, on the straight line to each seed attachment on the 5-m arc. Seed production (total number of seeds within 25 m of the trunk) was estimated by integrating the function describing mean abundance at each distance from the tree.

Levels of seed and egg predation at different distances from the edge were compared by logistic regression using GLIM 3.77 (Aitken, *et al.*, 1989).

RESULTS

Rio Bravo, Belize

A higher proportion of cardboard squares closer to the edge had ants (χ^2 = 11·85, d.f. = 2, p = 0·003). Peanut predation varied significantly with distance from the forest edge (χ^2 = 7·289, d.f. = 2, p = 0·02). Predation was significantly higher at 500 m than at the two other distances (both χ^2 = 4·21, d.f. = 1, p = 0·04; with continuity correction). At sites where there were few or no ants present (Table 1), the proportion of sites with one or more nuts taken also increased significantly with

Table 1. Observations at difference distances from the edge at Rio Bravo

Distance from edge	Eggs taken (out of 15)	Ants present (out of 50)	Two or more peanuts taken (out of 50)	One or more peanuts taken[a]	No peanuts taken[a]
30 m	10	44	8	3	7
100 m	13	38	8	10	11
500 m	1	29	18	23	7

[a] Observations of peanut predation counted only where few or no ants were present.

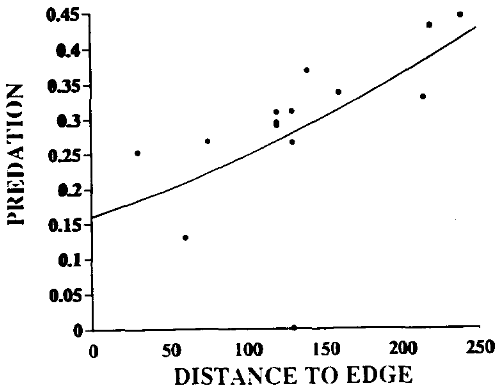

Fig. 1. Seed predation (proportion of experimental seeds eaten) as a function of the distance to the forest edge (in meters) for fourteen *Brosimum* trees at Los Tuxtlas. This edge effect explains a significant amount of residual variation after productivity (estimated number of seeds on the ground around each tree) has been accounted for. The graph and the data-points are standardized for productivity = 2000 seeds. The model with both productivity and distance accounts for about 44% of the variation; the distance effect explains about 26% of the residual variation when productivity is accounted for.

distance from the edge ($\chi^2 = 8{\cdot}473$, d.f. = 2, $p = 0{\cdot}01$). Squares located 30 and 100 m from the edge had lower predation rates than the 500 m sites ($\chi^2 = 5{\cdot}275$, d.f. = 1, $p = 0{\cdot}02$ and $\chi^2 = 4{\cdot}21$, d.f. = 1, $p = 0{\cdot}04$, respectively; with continuity corrections).

There was also a clear effect of distance from the edge on egg predation ($\chi^2 = 20{\cdot}893$, d.f. = 2, $p = 0{\cdot}0001$). Egg predation was lower 500 m from the edge than at 30 and 100 m ($\chi^2 = 9{\cdot}187$, d.f. = 1, $p = 0{\cdot}002$ and $\chi^2 = 16{\cdot}205$, d.f. = 1, $p = 0{\cdot}001$, respectively).

Veracruz, Mexico

There was a substantial difference in seed predation between trees ($\chi^2 = 31{\cdot}16$, d.f. = 13, $p < 0{\cdot}005$). The proportion of seeds removed ranged from 4 to 50%. These differences were related to the local seed density and overall seed production, the distance to the nearest neighbor, and the distance from the tree to the edge of the forest. The effect of these and other variables affecting seed predation (distance to nearest neighbor, local seed density, distance from the parent tree, etc.) are described in detail elsewhere (Burkey, submitted).

The level of seed predation was negatively correlated with the abundance of seeds on the ground ($\chi^2 = 11{\cdot}7$, d.f. = 1, $p < 0{\cdot}001$). Having controlled for differences in seed abundance, there was a significant effect of distance from the forest edge ($\chi^2 = 5{\cdot}83$ d.f. = 1, $p < 0{\cdot}025$)—despite the fact that the range of distances to the edge was small (30–240 m) and many of the trees were found at intermediate distances from the edge (Fig. 1). This matches the result from Belize. The null hypothesis of independence between distance to the edge and seed production was not rejected ($F(1,12) = 1{\cdot}516$, $p = 0{\cdot}24$).

DISCUSSION

I have demonstrated a qualitatively similar increase in seed predation moving from a man-made forest edge into the forest, at two different neotropical forest sites. In a 100-m edge zone at Rio Bravo, fewer peanuts and more eggs were removed than at 500 m into the forest. Ants appeared to be more abundant close to the edge. Because ants are such an important part of tropical forest ecosystems, both in terms of absolute numbers and biomass, their spatial distribution may have consequences for the plants they prey upon.

Egg predation seems to be more intense in a 100-m zone near the edge. It is likely that the most important egg predators are generalist species, like foxes *Urocyon cinereoargenteus* and coatis *Nasua nasua*, which skirt the edges and usually do well in modified habitats (Whitcomb *et al.*, 1976; Gates & Gysel, 1978; Chasko & Gates, 1982). Other potential mammalian egg predators in the Rio Bravo area are the tayra *Eira barbara* and the opossums (primarily *Didelphis virginiana* and *Philander opossum*). Remains of the eggs were not found, as one might expect if the predators had been birds. Higher egg predation rates near edges may have consequences for bird species in fragmented tropical habitats (Ricklefs, 1969; Skutch, 1985). In the temperate zone, increased nest predation along habitat edges has been reported by Gates and Gysel (1978), Chasko and Gates (1982), Brittingham and Temple (1983), Andrén *et al.* (1985), Wilcove *et al.* (1986), and Andrén and Angelstam (1988). Levenson (1981), Wilcove (1985) and Small and Hunter (1988) found increased predation in small as opposed to large forest fragments. Yahner and Wright (1985) and Angelstam (1986), however, found no effect of distance to the forest edge.

The prevailing explanation for increased predation near forest edges has been the high concentration of predators based in the surrounding farmland entering the forest to forage (e.g. Angelstam, 1986; Andrén & Angelstam, 1988; Small & Hunter, 1988). At the Belize site there was no surrounding farmland, but merely a road separating two tracts of previously continuous forest. Thus, it appears that the edge zone itself is used extensively by some egg predators, maybe as a travel corridor. In addition, many potential egg predators in the tropics are scansorial (climbing) and may favor the tangled and dense vegetation of the forest edge (e.g. opossums and kinkajou *Potos flavus*).

Seed predation may be lower in edge habitats than in the forest interior, because seed predators are edge-averse or are kept at low densities by predators. The most likely mammalian seed predators in the Rio Bravo area are spiny pocket mice *Heteromys desmarestianus*, rice rats *Oryzomys couesi* and *O. melanotis*, big-eared climbing rats *Ototylomys phyllotis*, and vesper rats *Nyctomys sumichrasti* (Timothy MacCarthy, pers. comm.). At Los Tuxtlas, the small mammal fauna is relatively complete, despite the small size of the remaining forest and contemporary loss of some large mammal species (Dirzo Miranda, 1991). The most important seed predators in the area are agoutis *Dasyprocta mexicana*, spiny pocket mice *Heteromys desmarestianus*, and Deppei's squirrel *Sciurus deppei*. Mexican deer mice *Peromyscus mexicanus* are common, but highly arboreal and eat few seeds on the ground (Rodolfo Dirzo, pers. comm.). If indeed tropical seed predators are scarcer in the edge zone, then habitat fragmentation would adversely affect their populations.

Although several studies have addressed egg predation in terms of distance from the forest edge (all temperate zone), no comparable study of seed predation is available (see Sork, 1983). Here I addressed both, and found an inverse relationship between egg and seed predation. At 30 m from the edge, the forest was very dense and tangled, but at 100 m it was indistinguishable from the forest at 500 m. Egg and seed predation at both these distances were significantly different from 500 m, so the edge effect was not merely an effect of forest cover or density.

This experiment should be replicated in time and space to test the generality of the results, and to elucidate the causal mechanisms. Since I was concerned with relative and not absolute predation pressures, the use of 'alien' seeds and eggs should not be critical unless there was some interaction term in the distance to edge effect. The results from Los Tuxtlas, using locally abundant seeds, support this view. Given the fragmented nature of the forest at Los Tuxtlas, and the small range of distances from the edge that could be studied, I was greatly surprised that an edge effect could be detected at all at this site. In the interests of preserving remnant patches of rainforest, it is important to determine how far into the forest edge effects of this type can be detected.

Habitat fragmentation and consequent edge effects can have far-reaching effects on the entire community. Spatial heterogeneity in seed predation may influence plants' recruitment. A reduction of seed predation in edge habitats may significantly alter the species composition of trees in the area, with possibly serious repercussions in the community (see Ranney *et al.*, 1981). Similarly, changes in the bird community may result from the change in egg predation. A subdivided reserve may eventually look entirely different from a large continuous reserve. Spatial variation in seed and egg predation resulting from increased edges can have complex and unexpected effects on the forest community. Tree species are no doubt differentially susceptible to seed predation, and changes in seed predation pressures may potentially alter the outcome of competitive interactions between tree species.

Since the edge in the Belize study was in fact a minor road with forest on both sides, the trends observed should be considered conservative estimates. With increased distance from other patches, foraging raids from neighboring patches would be less common, and microclimate changes in the edge zone (Lovejoy *et al.*, 1986) would be more pronounced. Furthermore, the road can hardly be considered a neighboring habitat from which competitors will interfere (see Janzen, 1983). For local seed trees, seed loss to a hostile environment may be lower when the edge is only a road. My results indicate, however, that even a minor dirt road through a reserve or wilderness area can have an effect on seed and egg predation, and presumably on the population biology of the trees and birds whose seeds and eggs are being eaten — as well as on the predators themselves.

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