

Egg and seed removal at urban and suburban forest edges

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Predation rates of natural and artificial bird nests in rural landscapes have been the subject of numerous studies, often in the context of proximity to edge. Similar studies in urban and suburban landscapes are lacking. We carried out a study of egg and seed removal at forest reserve edges in three urban and two suburban forests in and near New York City in 1994–1995. Few significant edge effects were found, but this may have been because of the extraordinarily high rates of egg and seed removal. Daily removal rates were higher in suburban sites (eggs, 86%; seeds, 95%) than in urban sites (eggs, 64%; seeds, 88%). Exposed seeds and eggs suffered higher rates of removal than seeds and eggs covered by leaf litter. Despite statistically significant differences among treatments, all of these rates would be prohibitively high if experienced by ground-nesting birds or large-seeded trees (if removal was associated with predation). A survey of the literature suggests that egg predation rates are prohibitively high in cities and peak in suburban sites (at least in this study), then drop rapidly in ex-urban and rural sites, perhaps because of a similar pattern in the abundance of corvid bird predators.

Keywords: landscape mosaic; nest predation; ex-urban; corvid; urban-rural gradient

Introduction

Where two communities or land uses meet, they form an edge that can appear abrupt. However, the effects of adjacent communities can penetrate into each other, often deeply. These edge effects may influence the management and restoration of habitats in fragmented landscapes, and can also degrade the viability of habitat fragments in landscape mosaics. In particular, small or narrow landscape patches can run the risk of being “all edge” (Alverson *et al.*, 1988, 1994).

Edge effects have been measured in many landscapes (see review Murcia, 1995). One of the most well-documented classes of edge effects concerns the predation of natural and artificial bird nests (reviewed in Paton, 1994; Andren, 1995). Although there is considerable variation among studies, eggs nearer edges often experience greater predation rates than eggs in the interiors of fields and forests. Such edge effects may explain greater rates of nest predation and nest parasitism in smaller forest fragments, where a greater proportion of land is near edges (Robinson *et al.*, 1995).

Seed removal rates can be estimated using methods similar to those used to estimate egg predation rates. However, edge effects on seed removal have been examined much more rarely than edge effects on egg predation. Limited studies suggest that seed removal is lowest at forest edges, and greatest in forest interiors (Burkey, 1993; Young, 1995), a pattern opposite that documented for eggs (but see Myser and Pickett, 1993).

Most edge effects have been measured in rural landscapes. However, suburban and urban landscapes are some of the most fragmented, and often include reserves of “natural” vegetation. In addition, these landscapes often have elevated densities of species, such as cats, crows, and deer, that can have a strong

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negative influence on native biodiversity. Studies of edge effects in urban and suburban landscapes are rare (Matlack, 1993; Young, 1995). Egg and seed removal studies in these ecosystems are completely lacking. In this study, we examined seed and egg removal rates with respect to proximity to edge in suburban and urban forests in the vicinity of New York City.

Study sites

We carried out this research in 1994–1995 in three urban forests and two suburban forests in New York state. We follow McDonnell and Pickett (1991) and Pouyat and McDonnell (1991) in these land-use classifications, based on human density and distance from Manhattan. Plant nomenclature follows Gleason and Cronquist (1991). New York Botanical Garden Forest in the Bronx is a 16-hectare (ha) uncut urban forest located on the slopes of the Bronx River. Dominant trees are hemlock (*Tsuga canadensis*), sugar maple (*Acer rubrum*), beech (*Fagus grandifolia*), and red oak (*Quercus rubrum*). Pelham Bay Park in the Bronx is 1105 ha, of which 313 ha are urban forest. The site chosen was a 40-ha forest on Hunter Island. Dominant trees are white poplar (*Populus alba*), black cherry (*Prunus serotina*), sassafras (*Sassafras albidum*), white oak (*Q. alba*), and red oak. Van Cortland Park in the Bronx is 458 ha, of which more than half is urban forest. The study site was in the 75-ha Northwest Forest. Dominant trees include tulip poplar (*Liriodendron tulipifera*), oak (*Quercus* spp.), hickory (*Carya* spp.), and sugar maple.

Marshlands Conservancy in Rye is a 64-ha reserve of oak-maple suburban forest, salt marshes, and old fields. Edith G. Read Natural Park and Wildlife Sanctuary in Rye is a 68-ha suburban forest along Long Island Sound. It is dominated by black birch (*Betula lenta*).

Study methods

All edges were at the interface of mown lawns and forest. We used uncracked English walnuts and chicken eggs because these were readily available, and could be easily distinguished from native species (but see our caveats in the Discussion). As suggested by Paton (1994), we examined removal within 100 m of forest edges, and at relatively short spatial intervals into each forest.

At each forest edge, two line transects were laid out from the forest edge toward the forest interior. Initially, orange flagging was placed at 0 m, 5 m, 10 m, 20 m, 40 m, 60 m, 80 m, and 100 m. At each distance along each transect, one pile of prey items was placed 2 m to the left and to the right of the flag. Each egg pile contained three eggs, and each seed pile contained four walnuts. Initially, eggs and seeds were alternated along each transect. In addition, covered and uncovered piles were alternated. Uncovered piles were simply laid on top of the leaf litter. Covered items were placed on top of the leaf litter, with additional leaf litter placed on top of them so that they were no longer visible.

Later, several changes were made in this design because 1) the possibility that birds and squirrels could be using the orange flagging to find prey items (see Haskell, 1996), and 2) prey items, especially those that were covered, were often difficult to relocate. The flagging was replaced by 10-cm uncolored wooden stakes driven into the ground until only a few centimeters were exposed. Additional stakes were placed 2 m to either side at the site of prey items. In this later design, each transect was dedicated to either seeds or eggs, and each side of each transect was dedicated to either covered or uncovered prey items. These two experimental designs produced similar results, and are combined here.

Also, we originally placed food items at 5 m, 10 m, and 20 m away from the forest edge into the adjacent mown grass. However, these experienced high levels of human interference, and this part of the experimental design was abandoned.

All prey items were resurveyed daily (if possible) until at least half of the food items along a transect had been taken. Removal rates were so high that this invariably happened by the first resurvey. Any eggs or walnuts that were partially damaged or eaten were counted the same as items completely missing.

At each forest edge, three to seven separate trials were run at different dates; one to three in November and December 1994, and two to four in March and April 1995. A total of 1536 seeds and 1152 eggs in 384 piles each were monitored at eight distances from two replicate forest edges in each of the three urban and two suburban forests.

Separate trials on different dates were treated as replicates within a forest. Regression analysis examined the relationship between removal rate and distance into the forest. For each forest, egg and seed removal rates were analyzed separately, and the two exposure classes were lumped.

When this analysis revealed few edge effects, data across all distances were lumped, and two-way analyses of variance (ANOVA; Model I) were done on the effects on removal rate of exposure (covered vs. exposed), and forest type (urban vs. suburban), blocked by individual forest (Zar, 1984). Eggs and seeds were analyzed separately.

Results

In almost every experimental run, the site was visited within 24 hours of the time the items were put out. Invariably, more than half of the items had disappeared, and often all were gone. In some cases, crows (*Corvus brachyrhynchos*) and squirrels (*Sciurus* spp.) began eating eggs and seeds even before the experimenter had left the area.

Of the five forests, one had more seed disappearance near the forest edge, and another had more egg disappearance near the forest edge (Table 1). However, neither of these patterns was statistically significant when inflation for multiple tests (across the five forests) was taken into account (Dunnett's *q* tests; Zar, 1984; pp. 317–318).

Across all forests and combining exposure categories, there was no significant pattern of seed or egg removal with respect to distance from forest edge ($p \sim 0.69$ for seeds, $p \sim 0.22$ for eggs). However, among covered eggs (across forests), significantly more were eaten nearer the forest edge than into the forest interior (Table 1).

In the suburban sites, 95% of the seeds and 86% of the eggs were removed (Fig. 1). This removal rate was greater (Table 2) than in the urban sites, where 88% of the seeds and 64% of the eggs were removed. Exposed items were removed at a significantly greater rate than covered items, for both eggs (89% vs. 60%) and seeds (95% vs. 87%). In both cases, these effects were stronger (and significant "Interaction")

Table 1. Regression analysis of removal rates and distance into forest from edges*

Forest	Seeds		Eggs	
	r	p	r	p
Botanical Garden (u)	-0.07	0.50	-0.11	0.26
Pelham Bay (u)	-0.03	0.81	-0.35	<0.02
Van Cortland (u)	-0.31	<0.02	+0.07	0.61
Read Sanctuary (s)	+0.04	0.69	+0.12	-0.26
Marshlands (s)	+0.04	0.75	+0.18	0.11
All forest combined				
All items	-0.02	0.69	-0.06	0.22
Covered items	-0.04	0.61	-0.51	<0.05
Exposed items	+0.002	0.97	+0.06	0.41

*u = urban; s = suburban. Neither of the two 'significant' patterns within individual forests remained statistically significant when corrected for multiple comparisons (Dunnett's *q* tests; Zar, 1984; pp. 317–318). Degrees of freedom varied between 22 and 54.

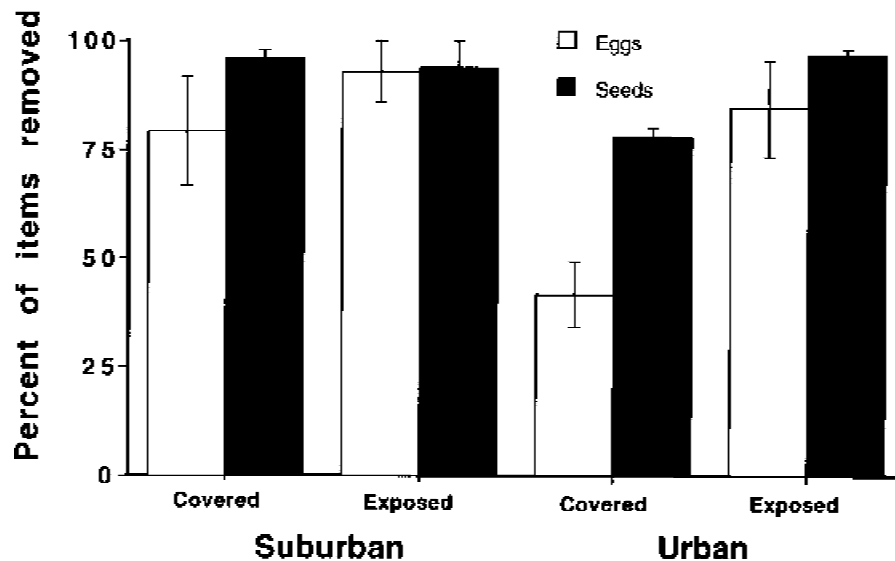


Figure 1. Mean daily removal rates (\pm one standard error) on covered and exposed piles of chicken eggs and walnuts in urban and suburban forests, averaged over all survey dates and all distances from the forest edges. Sample sizes were three urban and two suburban forests.

term in the ANOVA for seeds) in urban than in suburban sites (Fig. 1; Table 2), perhaps because the high removal rates of prey items in suburban sites left less room for variation in those rates.

Discussion

Experiments with artificial ground nests and seed piles can provide information on the risks experienced by ground-nesting birds or by large-seeded tree species. However, several caveats apply. First, we used chicken eggs (following Andren and Angelstram, 1988) and English walnuts as our baits, both of which are not native species, and both of which are larger and more conspicuous (when exposed) than the seeds and eggs of most of the relevant native species. If their size reduced the variety of animals that could

Table 2. Results of ANOVA for the number of eggs or seeds removed

Source	Degrees of freedom	Sum of squares	F ratio	p
Seeds				
Covered/exposed	1	166	8.07	<0.03
Urban/suburban	1	128	6.22	<0.05
Land use \times exposure interaction	1	280	12.62	<0.02
Error	6	123		
Eggs				
Covered/exposed	1	1923	7.73	<0.04
Urban/suburban	1	1264	5.08	<0.07
Land use \times exposure interaction	1	508	2.04	~0.20
Error	6			

remove them (see Haskell, 1995a, b), then the extraordinarily high removal rates observed here would be underestimates. On the other hand, their increased visibility may have increased removal rates. However, the removal rates of covered items was also exceedingly high, with even the slowest (>40% per day on covered eggs in urban forests) being at the extreme upper end of values reported in the literature (Table 3). Similarly, studies have suggested that predation rates on artificial nests are not necessarily good indicators of predation rates on natural nests, but again, these biases tend to *underestimate* actual predation risks (Willebrand and Marcstrom, 1988; Guyn and Clark, 1997). Second, damaged items were classified as “removed,” which we considered appropriate because they were no longer viable. Third, all of these items were placed in piles on the ground, so we do not have any assay of the effects of location on removal, or their relevance to birds that do not nest on the ground.

Egg disappearances were almost certainly caused by egg predation, but seed disappearances may also have been caused by removal to other sites, and some may have been cached uneaten (and therefore potentially viable). Direct observations suggest that most eggs were removed by crows (*C. brachyrhynchos*), and most seeds by squirrels (*Sciurus* spp.). However, we can not discount the possibility of removal at night by coyotes (*Canis latrans*), cats (*Felis domesticus*), raccoons (*Procyon lotor*), or skunks (*Mephitis mephitis*), all of which are present in suburban forests. An additional proviso: these experiments were done in late fall and early spring, times that do not directly correspond to the nesting and seed dispersal times of local species.

Covered seeds and eggs suffered lower disappearance rates than uncovered items, implying that some of the animals removing these items were using visual cues. However, substantial proportions of the covered items were also removed. Covered seeds suffered lower predation in a similar study in a rural forest to the north (Myster and Pickett, 1993).

With a few exceptions, we found no significant edge effects; seeds and eggs suffered similar disap-

Table 3. Summary of experiments on predation rates of artificial ground nests or egg piles in temperate forests*

Forest type	N	Estimated daily removal rate overall (%)	Reference
Urban	208	67	This study
Suburban	176	87	This study
Ex-urban	32	15–30	Young, 1995
Ex-urban	58 (4 d)	14	Nour <i>et al.</i> , 1993
Ex-urban	58 (8 d)	14	Nour <i>et al.</i> , 1993
Ex-urban (A)	93	43	Andren, 1992
Ex-urban (A/F)	100	35	Andren, 1992
Rural (F/A)	98	28	Andren, 1992
Rural (F)	143	20	Andren, 1992
Rural	84 (7 d)	3	Wilcove <i>et al.</i> , 1986
Rural	40 (14 d)	8	Wilcove <i>et al.</i> , 1986
Rural	40 (25 d)	6	Wilcove <i>et al.</i> , 1986
Rural	>5000	2–10	Robinson <i>et al.</i> , 1995
Rural	298	1–2	Vanderhaegen and DeGraaf, 1996
Rural		1–6	DeGraaf and Angelstam, 1993
Rural	300	5	Yahner and Mahan, 1996

*N is the number of “nests.” Nour *et al.* (1993) described their study site as “an agricultural matrix near Antwerp, Belgium” and “a West European agricultural to suburban landscape,” which I have classified as ex-urban. In the Andren (1992) study, “A” stands for agricultural, and “F” stands for forested (his designations).

pearance rates at all distances from forest edge to forest interior. However, among covered eggs, significantly more were taken from near edges than from deeper in the forest interior. This is consistent with previous studies in which eggs were often found to be at greater risk near forest edges (reviewed in Paton, 1994, but see Andren, 1995 for counter-examples), and with the observation that birds in smaller forest fragments experienced more natural nest predation than did birds in larger forest fragments (Robinson *et al.*, 1995).

The lack of more general or stronger edge effects may have been because of the extraordinarily high removal rates in these urban and suburban sites. In most cases the large majority of seeds or eggs were eaten in the first 24 hours. These removal rates are all the more extraordinary if our use of larger eggs (see above, and Haskell, 1995a, b) or artificial nests (Willebrand and Marcstrom, 1988, Guyn and Clark, 1997) decreased the number of species preying upon them. Even if there were edge effects that could have been measured on a finer temporal scale, they are unlikely to be biologically interesting, because both seeds and eggs would need to be in the environment for more than a few days before hatching or germinating.

To our knowledge, this is the first study of seed and egg removal at urban and suburban forest edges. The overall removal rates for both seeds and eggs were significantly higher in suburban than in urban forests. Most likely, the animals that prey upon seeds and eggs reach maximum levels in suburban (and urban) sites, which have a rich mixture of human settlement and open space. In Sweden, densities of corvid birds (crows and relatives) increased along a gradient from rural forest to agricultural sites near a city, but no urban estimates were made (Andren, 1992). In California, the abundance of corvids (scrub jays, *Aphelocoma coerulescens*) along an urban-rural gradient peaked in suburban sites (Blair, 1996). These high predation rates may explain the relative paucity of terrestrial birds in urban and suburban environments (Emlen, 1974; Sodhi, 1992). In Virginia (approximately 200 miles south of our study area, in similar habitats), Bowers and Breland (1996) found significantly higher seed removal rates by gray squirrels (*Sciurus carolinensis*) in urban and suburban sites than in rural agricultural and forest sites. Other wild animals should also be more abundant in suburban than in urban forests.

The data in Table 3 come from different studies using different methodologies that would be expected to affect their results in different ways, increase variance, and reduce the probability of finding patterns. Nonetheless, there appear to be consistent differences in egg predation rates across this urban-rural gradient (Fig. 2). Removal rates at all sites in this study were far higher than those reported in ex-urban and rural sites (Table 3). In a study of seed and egg removal with similar methodology in a nearby ex-urban site in Armonk, New York, it took two to four days for approximately half the seeds or eggs to disappear (Young, 1995). Here we use the term “ex-urban” to refer to areas that are partially residential, but with forest cover greater than 50%.

In several studies in rural deciduous forest sites in the eastern United States, it took 7 to 14 days for half of the eggs to disappear, at an average of 3–8% per day. Similarly, an extensive study of hundreds of natural nests in forest fragments in rural midwestern United States revealed daily predation rates of 2–10% (Robinson *et al.*, 1995). We do not yet have studies of seed removal in rural forest fragments.

Egg predation is higher in smaller forest fragments than in larger forest fragments (Telleria and Santos, 1992; Robinson *et al.*, 1995), perhaps because of greater egg predation near forest edges (Paton, 1994; Murcia, 1995). However, the variation in predation rates across land uses in Table 3 is not likely to be caused by variation in forest size; the urban and suburban forest patches studied here and in the “ex-urban” sites were relatively large (16–314 ha, all but one >60 ha).

Overall, the results in Table 3 imply that egg (and seed?) predation rates are prohibitively high near cities and even higher in suburban sites (at least in this study), then drop rapidly in ex-urban and rural sites (Fig. 2). This pattern may parallel a similar pattern of corvid abundance along the urban-rural gradient, such as that found for scrub jays (*Aphelocoma coerulescens*) in California (Blair, 1996). An

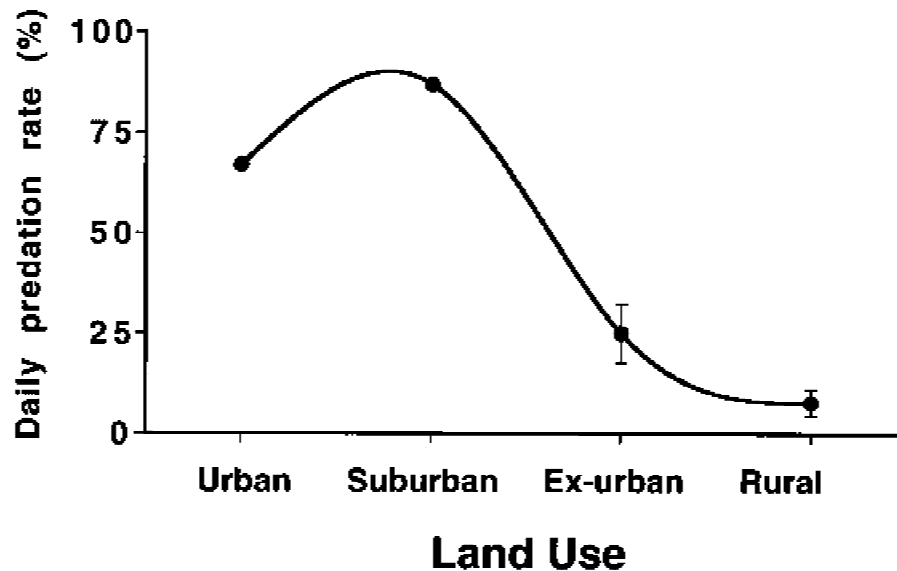


Figure 2. Relationship between mean daily predation rate and intensity of land use, based on this study and a review of artificial ground nest studies (see Table 3). Bars represent one standard error, with the mean value for each study being a sample point ($n = 1, 1, 3, 6$, respectively). Curve fit using “extrapolation” feature of Cricket Graph III.

analysis of published nest predation studies suggested that predation rates were higher in more deforested landscapes (Hartley and Hunter, 1996). Urban and suburban forest ecosystems may be highly inhospitable places for offspring recruitment for both large-seeded trees and ground-nesting birds.

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