Evidence of an Edge Effect on Avian Nest Success

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Abstract: *Habitat fragmentation may modify ecological patterns by increasing the importance of edge effects, including elevating rates of predation on avian nests. Conventional wisdom suggests an increased rate of predation along habitat edges, and previous reviews support this view. These reviews did not apply recent statistical approaches, however, and some were based on a small number of studies. In our meta-analysis of 64 nest-predation experiments, our results supported prior reviews of the general pattern of increased nest predation along habitat edges (* $p < 0.01$ *). We separated studies into ecologically relevant categories and found the following patterns: (1) Edge effects were more pronounced in North America and northwestern Europe than in central Europe or Central America. This result may be biased, however, by the different habitats studied in the regions. (2) Marshes and deciduous forests had significant edge effects, whereas edge effects were not apparent in coniferous forests, tropical forests, or fields. (3) Ground and natural nest studies were more likely to exhibit edge effects. (4) Edge effects were detected in studies that used quail eggs and real eggs. (5) Edge effects were not significant when artificial nests were exposed for typical incubation periods, but were significant for shorter exposures. Three alternative hypotheses may explain increased nest predation along edges. The edge-effects hypothesis states that increased nest losses along edges are the result of the habitat discontinuity. The landscape-structure hypothesis states that more fragmented landscapes are more heavily depredated by nest predators. The human-disturbance hypothesis states that near anthropogenic edges increased nest predation is related to human activities. Nest-predation experiments should be placed in a landscape context to reveal differences between the hypotheses.*

Key Words: edge type, edge width, effect size, landscape type, nest predation, review

Evidencia de un Efecto de Borde Sobre el Éxito de Nidos de Aves

Resumen: *La fragmentación del hábitat puede modificar patrones ecológicos al incrementar la importancia de los efectos de borde, incluyendo el incremento de las tasas de depredación de nidos de aves. Convencionalmente se cree que existiría un incremento en la tasa de depredación a lo largo de los bordes de hábitat y revisiones previas apoyan esta opinión. Sin embargo, estas revisiones no aplicaron métodos estadísticos recientes y algunos se basaron en un número pequeño de estudios. En nuestro meta-análisis de 64 experimentos de depredación de nidos, nuestros resultados apoyaron revisiones previas del patrón general de incremento de depredación de nidos a lo largo de bordes de hábitat (* $p < 0.01$ *). Separamos a los estudios en categorías ecológicamente relevantes y encontramos los siguientes patrones. (1) Los efectos de borde fueron más pronunciados en Norte América y el noroeste de Europa que en Europa central o América Central. Sin embargo, este resultado puede estar sesgado debido a los diferentes hábitats estudiados en las regiones. (2) Las marismas y los bosques deciduos tuvieron efectos de borde significativos, mientras que los efectos de borde no fueron aparentes en bosques de coníferas, bosques tropicales o campos. (3) Estudios de nidos naturales y terrestres fueron más propensos a presentar efectos de borde. (4) Se detectaron efectos de borde en estudios que utilizaron huevos de codorniz y huevos reales. (5) Los efectos de borde no fueron significativos cuando se expusieron nidos artificiales por períodos de incubación típicos, pero fueron significativos para exposiciones más cortas.*

Hay tres hipótesis alternativas que pueden explicar el incremento de depredación a lo largo de bordes. La hipótesis de los efectos de borde enuncia que el aumento en la pérdida de nidos a lo largo de bordes es el resultado de la discontinuidad del hábitat. La hipótesis de la estructura del paisaje enuncia que los paisajes más fragmentados son depredados más intensamente por los depredadores de nidos y la hipótesis de perturbación humana señala que el incremento de depredación de nidos cerca de bordes antropogénicos está relacionado con estas actividades. Los experimentos de depredación de nidos deberían ser colocados en un contexto de paisaje para descubrir las diferencias entre las hipótesis.

Palabras Clave: amplitud de borde, depredación de nidos, efecto de tamaño, revisión, tipo de borde, tipo de paisaje

Introduction

Habitat fragmentation is one of the main causes of the recent impoverishment of biodiversity (Vitousek et al. 1997). Habitat fragmentation—that is, the conversion of a formerly continuous habitat into small, isolated remnant patches (e.g., Meffe & Carroll 1997), results in the loss of wildlife habitat and increasing amounts of habitat edges within the landscape. Edges may alter the distribution, abundance, and behavior of organisms, which has been termed the edge effect (Murcia 1995). The consequences of habitat fragmentation and related edge effects can be substantial. For example, the continental-scale decline of some Neotropical migrant birds in northeastern America has been attributed in part to increased nest predation and cowbird parasitism near edges (Brittingham & Temple 1983; Wilcove 1985; Askins 1995; Robinson et al. 1995). Indeed, pioneering work on nest predation in forests showed higher nest-predation rates at habitat edges than in interior habitats (Gates & Gysel 1978; Chasko & Gates 1982; Wilcove 1985; Wilcove et al. 1986; Andrén & Angelstam 1988). More recent reviews also concluded that increased nest predation at the edges is commonly occurring across many landscapes (Paton 1994; Hartley & Hunter 1998).

Nest predation is important because the loss of nests and broods is the main cause of reproductive failure in birds (Ricklefs 1969; Martin 1995, 1996), representing roughly 30% of failure events (Martin 1995; Martin & Clobert 1996; Báldi 1999). Not surprisingly, the number of studies of nest predation in relationship to edges increased after these pioneering studies in which either real or artificial nests were used.

Paton (1994) used a large data set of 41 experiments to calculate likelihood-ratio chi square for each experiment and summarized the results with a "vote-counting" approach. Hartley and Hunter (1998) used Fisher's exact test for each experiment and the vote-counting method, but on a smaller data set. There are two limitations to vote-counting analyses. First, conventional null hypothesis significance tests are not adequate because one expects a priori the rejection of the null hypothesis (Anderson et al. 2000; Guthery et al. 2001); that is, we expect higher

depredation rates near edges. The biologically meaningful issue is not to test an uninformative null hypothesis, but rather the magnitude of the effect (Gurevitch et al. 1992; Johnson 1999). Second, the vote-counting method is the simplest method of synthesizing multiple experiments and can produce seriously biased results, may have low statistical power, and may fail to provide critical information on the overall results of the reviewed studies (Gurevitch & Hedges 1999).

In our review, we used a meta-analysis in which independent studies are synthesized quantitatively, which provides interpretation of the strength of the statistical findings based on the magnitude of the overall effect size (Gurevitch & Hedges 2001). Our main aims were to (1) conduct a meta-analysis of the primary edge-effect studies to test whether nest-predation rates were higher near edges than in the interior; (2) explore edge-effect patterns across geographical locations, vegetation types, nest and egg types, and exposure times; and (3) quantify how nest-predation rates changed in relation to distance from the edge.

Methods

We used three data sets in our meta-analysis: (1) a set of peer-reviewed papers chosen based on an extensive literature search of the years 1972–1999 in three large databases (Ecology Abstracts, Biosis, and ISI); (2) data from our own published and unpublished experiments; and (3) studies used by Paton (1994), although we excluded three of the papers Paton used that presented insufficient data for our analysis. We selected studies that measured nest predation and provided information on distance from edges. We included experiments with both artificial and real nests. For comparative purposes, artificial nests are usually useful substitutes for real nests (Major & Kendal 1996). Due to the large diversity of experimental designs, we recalculated nest-predation estimates for all studies to obtain reliable and comparable results. We used the original number of nests and number of depredated nests for calculations, with data often

extrapolated from figures. For studies that reported more than one experiment, we treated each experiment as an independent study. We estimated effect size with the following procedure. First, we compiled a database containing the number and percentage of depredated nests in relation to distance from the edge. Second, we conducted a likelihood-ratio chi-square (G) test for each experiment to determine the statistical significance of homogeneity of predation across the edge. Third, we followed methods outlined by Rosenthal and DiMatteo (2001) and Jennions and Møller (2002*a*) to calculate the standard normal deviate (Z) from p values. We used the Z values and the sample sizes (number of nests) to calculate the correlation coefficient, and then we transformed the correlation coefficient to normalize the distribution with Fisher's z transformation. Fisher's z transformation estimates effect size and thus provide a basis for the summary meta-analysis (Rosenthal 1991; Gurevitch et al. 1992; Rosenthal & DiMatteo 2001). The effect size was positive if predation was higher near edges. The data followed a normal distribution, as required by meta-analysis. For this meta-analysis, we used MetaWin 2.0 (Rosenberg et al. 2000), which has been used by a number of investigators (e.g., Merila & Crnokrak 2001; Suding 2001; Wan et al. 2001; Koricheva 2002). We used mixed-effects models, which assumed that the studies shared a common mean effect, that there was random variation among them, and that they showed sampling variation. Therefore, the effect size of a particular study is composed of a "fixed" part that is characteristic of all analyzed studies (e.g., all herbivores share certain characteristic responses) and another part that is characteristic of the one study in which the character differs at random from other studies (Gurevitch & Hedges 2001).

To better understand the variations in edge effect, we segregated experiments into several categories, including geographical location, landscape type, vegetation type of studied edges and that of the adjoining edges, nest and egg type, and exposure time (Table 1). We investigated how much nest predation increased for each unit change in distance to an edge. We analyzed all experiments that had nests at the very edge (0 m) and nests toward the interior. We then analyzed all experiments that had nests 0–24 m from the edge and farther toward the interior. Then we excluded nests in the 0- to 24-m belt along the edge and included only those experiments in which nests were placed 25–49 m from the edge and farther toward the interior. In this way we shifted the edge by 25-m increments and monitored the changes in the magnitude of the edge effect.

We tested Angelstam's (1986) hypothesis, which suggests that edge effects are most likely to occur where there are marked contrasts in the productivity gradient between the habitat patch and its matrix (sharp edges such as forest to field, field to forest, or marsh to water) and are less likely to occur if this gradient is less pro-

nounced (soft edges such as forest to forest and field to field).

A key question in this type of meta-analysis is the file-drawer problem—that is, the fact that studies with nonsignificant results are often not published (Rosenberg et al. 2000; Møller & Jennions 2001). The publication bias of positive results is so pronounced that there is a positive correlation between effect sizes and journal quality (Murtaugh 2002). To determine whether a publication bias exists in the literature on nest predation and edge effects, we used funnel plots to graphically explore meta-data, plotting the effect size of each individual experiment against its sample size (Palmer 1999). This is also known as the "trim and fill" method (Jennions & Møller 2002*b*). If there is no publication bias, plots are funnel-shaped because (1) studies with small sample sizes have increased sampling error, so the variation around the effect size should decrease as sample size increases, (2) effect size should be independent of sample size, and (3) individual studies should be normally distributed at a given sample size (Palmer 1999).

Results

Sixty-four experiments from 32 studies were included in our analysis (Table 1). All investigations were conducted in the Northern Hemisphere, mainly in temperate north and central Europe and North America. We evaluated 41 experiments in which edges were open habitats and 23 experiments in forested habitats. Open habitats were mainly fields and farmlands with low-intensity management, including natural grasslands (19 experiments) and marshlands and bogs (22 experiments). These habitats were surrounded by forests (24 experiments), intensively managed agricultural croplands (11 experiments), or open water (6 experiments). Forested habitats were coniferous forests (7 experiments), deciduous forests (12 experiments), or tropical forests (4 experiments). Fields (20 experiments) or secondary forests (3 experiments) surrounded these habitats.

The main predator species varied as a result of the large geographical scope of the review, but, as expected, corvids and small predatory mammals such as raccoons (*Procyon lotor*), red foxes (*Vulpes vulpes*), skunks (*Mephitis mephitis*), minks (*Mustela vison*), and weasels (*Mustela nivalis*) were the most common species (Table 1). Other small mammals (rodents), birds (gulls, raptors, small passerines), and snakes were also recorded as predators. Most of the predator identifications were based on nest remains or on the list of potential predators in the study area. Recently, there has been serious criticism of such indirect methods (Lariviere 1999; Williams & Wood 2002), so the reliability of the identity of nest predators

Table 1. Source and main characteristics of each nest-predation experiment considered.

Source	Location	Studied habitat	Studied edge	Other edge	Primary predators[a]	Type of nests (no. of nests)	Type of eggs	Exposure
Artificial nests								
Andrén & Angelstam 1988[b]	Sweden	open	field	forest	C1; PM; RF	ground (92)	chicken	less
Andrén & Angelstam 1988[b]	Sweden	forested	coniferous forest	field	C1; PM; RF	ground (88)	chicken	less
Angelstam 1986[b]	Sweden	forested	coniferous forest	field	C1; PM; RF	ground (150)	chicken	less
Avery et al. 1989[b]	Scotland	open	marsh	forest	C2; RF; Sh; St; WC	ground (1400)	chicken	less
Báldi & Batáry 2000 (2 exp.)[c]	Hungary	open	marsh	field	SsS	elevated (30, 30)	quail/plasticine	less
Báldi & Batáry 2000	Sweden	open	marsh	water	G; MH	elevated (45)	quail/plasticine	less
Báldi & Batáry 2000 (3 exp.)[c]	Hungary	open	marsh	water	C3; SR	elevated (50, 60, 60)	quail/plasticine	normal
Báldi, unpublished data, 1998	Hungary	open	marsh	field	ND	ground (60)	quail	normal
Báldi, unpublished data, 1998	Hungary	open	marsh	field	ND	ground (20)	chicken	less
Batáry et al. 2004	Austria	open	marsh	water	G; MH; SR	elevated (77)	quail/plasticine	normal
Berg 1996	Sweden	open	field	forest	ND	ground (105)	quail	normal
Berg et al. 1992[b] (6 exp.)[c]	Sweden	open	marsh	forest	ND	ground (96, 64, 40, 84, 88, 68)	quail	normal
Boag et al. 1984[b]	Alberta	forested	deciduous forest	forest	C4; DM; RS	ground (90)	quail	normal
Burger 1988[b]	Missouri	open	field	forest	C5; M1	ground (270)	quail	less
Burger 1988[b]	Missouri	forested	deciduous forest	field	C5; M1	ground (324)	quail	less
Carlson 1989[b] (2 exp.)[c]	Missouri	forested	deciduous forest	field	ND	ground (400, 200)	quail	less
Fazekas & Báldi 2000	Hungary	open	field	forest	MsS; SR	ground (48)	quail/plasticine	normal
Gibbs 1991[b] (2 exp.)[c]	Costa Rica	forested	tropical forest	forest	B; M2; Sn	ground (147, 120)	quail	less
Gibbs 1991[b] (2 exp.)[c]	Costa Rica	forested	tropical forest	forest	B; M2; Sn	elevated (147, 120)	quail	less
Møller 1989[b] (2 exp.)[c]	Denmark	open	field	forest	C6	ground (180, 180)	plasticine	less
Møller 1989[b] (2 exp.)[c]	Denmark	forested	coniferous forest	field	C6	ground (180, 180)	plasticine	less
Pasitschniak-Arts & Messier 1995	Saskatchewan	open	field	field	C5; Co; G; R; RF; SR; SS	ground (225)	chicken	normal
Pasitschniak-Arts & Messier 1996	Saskatchewan	open	field	field	C7; G; SS; UM	ground (360)	chicken	normal
Picman et al. 1993	Ontario	open	marsh	field	LtW; MW; R	elevated (53)	quail	less
Ratti & Reese 1988[b] (2 exp.)[c]	Idaho	open	field	forest	C8; Ch; RS	ground/elevated (180, 208)	quail	normal
Ratti & Reese 1988[b] (2 exp.)[c]	Idaho	forested	coniferous forest	field	C8; Ch; RS	ground/elevated (180, 201)	quail	normal
Söderström et al. 1998	Sweden	open	field	forest	B; C9; RF; SR	ground (114)	quail/plasticine	normal
Söderström et al. 1998	Sweden	open	field	forest	B; C9; RF; SR	elevated (114)	quail/plasticine	normal
Storch 1991[b]	Germany	forested	coniferous forest	field	C10; UM	ground (135)	chicken	normal
Wilcove et al. 1986[b]	Maryland	forested	deciduous forest	field	C11; Ch; RF	ground (84)	quail	less
Wilcove et al. 1986[b] (2 exp.)[c]	Maryland	forested	deciduous forest	field	C11; Ch; RF	ground (40, 40)	quail	normal
Natural nests								
Berg 1992 (3 exp.)[c]	Sweden	open	field	forest	ND	Curlew (84, 84, 91)		
Berg 1996	Sweden	open	field	forest	ND	Curlew (35)		
Berg 1996	Sweden	open	field	forest	ND	Lapwing (161)		
Best 1978[b]	Illinois	open	field	forest	Sn	Field Sparrow (135)		
Chasko & Gates 1982[b] (2 exp.)[c]	Maryland	forested	deciduous forest	field	C11; Ch; RF	songbirds (210, 136)		
Gates & Gysel 1978[b]	Michigan	forested	deciduous forest	field	C11; Ch; RF	songbirds (561)		

continued

Table 1. (continued)

Source	Location	Studied habitat	Studied edge	Other edge	Primary predators[a]	Type of nests (no. of nests)	Type of eggs	Exposure
Honza et al. 1998	Czech Republic	open	marsh	water	C12; MH; Sh; RS; SR; St; W	Reed Warbler (153)		
Kristiansen 1998	Denmark	open	marsh	field	C13; Mi; RF; WP	Gray-lag Goose (31)		
Pasitschniak-Arts et al. 1998/1[d]	Saskatchewan	open	marsh	field	C14; Co; G; LtW; R; RF; SS	Mallard (53)		
Pasitschniak-Arts et al. 1998/2[d]	Saskatchewan	open	marsh	field	C14; Co; G; LtW; R; RF; SS	Gadwall (50)		
Pasitschniak-Arts et al. 1998/3[d]	Saskatchewan	open	marsh	field	C14; Co; G; LtW; R; RF; SS	Blue-winged Teal (96)		
Temple & Cary 1988[b]	Wisconsin	forested	deciduous forest	field	ND	songbirds (276)		
Vickery et al. 1992[b]	Maine	open	field	forest	SS	songbirds (60)		
Yahner 1991[b]	Pennsylvania	forested	deciduous forest	field	C5	songbirds (95)		

[a]Abbreviations: B, badger (Meles meles); C, corvids (1, Corvus corax, C. corone cornix, C. monedula, Pica pica [Pp.]; 2, C. c. cornix; 3, C. c. cornix, P. p.; 4, Perisoreus canadensis [P.c.]; 5, C. branchyrhynchos [C.b.]; 6, C. c. cornix, P. p., Garrulus glandarius [G.g.]; 7, C. b., P. p.; 8, Cyanocitta stelleri, P. c., C. b., C. corax; 9, C. c. cornix, P. p., G. g.; 10, C. corax, C. c. corone, G. g., Nucifraga caryoctactes; 11, Cyanocitta cristata, C. b.; 12, C. c. cornix, G. g.; 13, C. c. cornix; 14, C. b., P. p.); Cb, chipmunk (Tamais spp.); Co, coyote (Canis latrans); G, gull species (Larus spp.); LtW, long-tailed weasel (Mustela frenata); HD, hazel dormouse (Muscardinus avellanarius); HM, harvest mouse (Micromys minutus); M, mammals (1, Didelphis virginiana, Procyon lotor, Mephitis mephitis, Sciurus carolinensis; 2, Nasua narica, Mustela frenata, Eira barbara, Potos flavus, Sciurus granatensis); Mt, mink (Mustela vison); MH, Marsh Harrier (Circus aeruginosus); MsS, medium-sized songbirds; MW, Marsh Wren (Cistothorus palustris); ND, no data; PM, Pine Marten (Martes martes); R, raccoon (Procyon lotor); RF, red fox (Vulpes vulpes); RS, red squirrel (Tamiasciurus hudsonicus); Sb, sparrowhawk (Accipiter nisus); Sn, snakes; SR, small rodents; SS, stiped skunk (Mephitis mephitis); SsS, small-sized songbirds; St, stoat (Mustela erminea); UM, unidentified mammals; W, weasel (Mustela nivalis); WC, wild cat (Felis sylvestris); WP, western polecat (Mustela putorius).

[b]Experiments from Paton (1994).

[c]Some experiments from a paper were combined, which is indicated after the reference.

[d]Numbering after the year of the citation refers to different experiments from the same paper.

may be low. Consequently, we did not analyze predator effect in detail. In addition, Chalfoun et al. (2002) recently reviewed the topic.

Nest survival was estimated based on artificial (47 experiments) or natural (17 experiments) nests. The latter studies monitored waterfowl, waders, and passerines (Table 1). Artificial open nests were located on the ground (32 experiments) or higher in vegetation (11 experiments). The exception was the study by Ratti and Reese (1988), which mixed the locations within four experiments. Thus, it was not possible to distinguish between ground and elevated nests. Most of these experiments used real quail or chicken eggs and/or plasticine eggs, with clutch size ranging from one to nine. Some investigators used supplemental plasticine eggs to aid in predator identification via tooth and beak marks. The exposure time of artificial eggs for most studies ranged between 7 and 14 days.

There was wide variation in experimental design and number of distance categories: about half the studies used only two categories (edge vs. inside), some did not put nests at the edge, and the distance between two distance categories also varied (Table 2). There was a significant positive edge effect, with more nests depredated near edges (Fig. 1).

We divided the 64 experiments into two to five groups within seven ecologically meaningful categories (Fig. 1). We detected an overall edge effect in experiments in North America and northwest Europe, but no edge effect was found in Central America and central Europe (Fig. 1). This may be a consequence of edge type, with studies in Central America investigating only forest edges and studies in central Europe mainly investigating marsh edges. The increased depredation along edges was similar in open and forested habitats. With better resolution, however, marsh and deciduous forest edges had increased nest losses compared with the interior habitats, whereas coniferous forests, tropical forests, and fields had no significant edge effect (Fig. 1). There appeared to be a strong edge effect in North American marshes but not in central European marshes.

The adjoining habitat to the studied edge ("other edge") was related to nest-predation edge effect only when the adjoining habitat was a field (Fig. 1). There was great variability in the results on nest and egg types. Ground and natural nest studies and studies with quail or real eggs generally showed edge effects (Fig. 1). Edge effects were not significant for artificial nests exposed for typical incubation periods but were significant when nests were exposed for shorter periods and when natural nests were used in experiments (Fig. 1).

Distance from edge had a significant effect on nest-predation rates. The largest effect size (i.e., the highest predation rate) was for nests in the 0- to 24-m distance category (Fig. 2). Edge effects disappeared when experiments with nests in the first 50 m of the edge were excluded. Therefore, edge effects were most pronounced within the first 50 m from the edge.

Our results confirmed Angelstam's (1986) hypothesis: edge effect occurred at sharp edges (mean effect size = 0.1033, df = 49, 95% confidence interval [CI] from 0.0455 to 0.1611) but not at soft edges (mean effect size = 0.1180, df = 13, 95% CI from −0.0087 to 0.2446).

Funnel plots indicated that there was no publication bias in the literature investigating nest-predation rates near edges (Fig. 3).

Discussion

We reviewed papers on the relationship between nest-predation rates and distance from an edge and applied a meta-analysis. Our results support past reviews that showed increased nest predation at habitat edges, primarily within 50 m of an edge (Paton 1994; Hartley & Hunter 1998). Therefore, edge effect should be incorporated into landscape planning (Laurance 2000). We also found no apparent publication bias in the peer-reviewed literature that we reviewed for our analysis.

Fragmentation of habitats leads to increases in the amount of edge habitat. A key question is the width of the edge effect: how large is the affected area? Most researchers found that the edge effect penetrates <150 m into forest fragments (Laurance 2000). Paton (1994) estimated that the edge effect of nest predation penetrates approximately 50 m into habitats. We also showed that nest predation declined from the edge to the interior and disappeared if the first 50 m was excluded. Laurence (2000) suggests that edge effects could occur over larger spatial scales, 1–5 km from the physical edge. Only two of the experiments we included used nests beyond 1 km (Table 2); therefore, our results are limited to a local spatial scale. However, results from both these studies showed significant edge effect, which may indicate that the nest-predation edge effect is not restricted to the local scale.

In the last few years, a number of investigators have synthesized the literature on edge effects. Paton (1994) concluded that nest predation increases in habitat edges and has been cited widely in the literature. Andrén's (1995) comprehensive review suggests that edges do not always generate increased nest predation. Hartley and Hunter (1998) conducted a meta-analysis of 13 studies and found that edge effect depends on the forest cover of the landscape. They suggest that predation rate is higher near edges in deforested than in forested landscapes (which result contradicts our findings and those of Andrén [1995]), but they reviewed only two studies from deforested landscapes. Manolis et al. (2000) found elevated predation rates near clearcut edges in their review of 26 experiments, but their analyses were geographically restricted to northern hardwood-conifer landscapes. More recently,

Table 2. Depredation rates and number of nests (%/N) as a function of distance from edge (e.g., 50/30 means that 50% of 30 nests were depredated).

Reference[a]	Distance from edge (m)											p (n)[e]	Zr ± CI[f]
	0	25	50	75	100	150	200	300	500	900	>1000		
Artificial nests													
Andrén & Angelstam 1988/1[b]	50/30	61/18			54/26			61/18				0.836 (92)	−0.0215 ± 0.0112
Andrén & Angelstam 1988/2[b]	50/30		33/21		13/24			8/13				0.004 (88)	0.3170 ± 0.0118
Angelstam 1986[b]			67/30				59/42		70/27	60/30	61/21	0.885 (150)	0.0118 ± 0.0068
Avery et al. 1989[b]					44/350				37/350	33/350	30/350	<0.001 (1400)	0.0882 ± 0.0007
Báldi & Batáry 2000/1	6/15		24/15									0.335 (30)	−0.4084 ± 0.0370
Báldi & Batáry 2000/2	6/15		47/15									<0.001 (30)	−0.6944 ± 0.0370
Báldi & Batáry 2000/3	73/22		22/23									<0.001 (45)	0.7126 ± 0.0238
Báldi & Batáry 2000/4	56/25		64/25									0.563 (50)	−0.0804 ± 0.0213
Báldi & Batáry 2000/5	40/30		47/30									0.602 (60)	−0.0674 ± 0.0175
Báldi & Batáry 2000/6	83/30		53/30									0.011 (60)	0.3409 ± 0.0175
Báldi unpublished 1998/1	63/30		47/30									0.193 (60)	0.1697 ± 0.0175
Báldi unpublished 1998/2	70/10			80/10								0.605 (20)	−0.1161 ± 0.0588
Batáry et al. 2004	85/39		34/38									<0.001 (77)	0.5076 ± 0.0135
Berg 1996/1[a]			66/50				71/55					0.588 (105)	−0.0528 ± 0.0098
Berg et al. 1992/1[b]			61/36				58/60					0.788 (96)	0.0274 ± 0.0108
Berg et al. 1992/2[b]			38/32				7/32					0.002 (64)	0.4074 ± 0.0164
Berg et al. 1992/3[b]			58/12				64/28					0.723 (40)	−0.0561 ± 0.0270
Berg et al. 1992/4[b]			35/40				61/44					0.015 (84)	−0.2719 ± 0.0123
Berg et al. 1992/5[b]			20/44				9/44					0.129 (88)	0.1633 ± 0.0118
Berg et al. 1992/6[b]			15/40				10/28					0.604 (68)	0.0630 ± 0.0154
Boag et al. 1984[b]	58/43	70/47										0.232 (90)	−0.1267 ± 0.0115
Burger 1988/1[b,c]		65/NA	37/NA									<0.001 (270)	0.2554 ± 0.0037
Burger 1988/2[b,c]		30/NA	11/NA									<0.001 (324)	0.2323 ± 0.0031
Carlson 1989/1[b,c]	95/NA		72/NA		64/NA		34/NA	23/NA	24/NA			<0.001 (400)	0.2084 ± 0.0025
Carlson 1989/2[b,c]						76/NA	72/NA					0.611 (200)	−0.0359 ± 0.0051
Fazekas & Báldi 2000	94/16		25/16				38/16					<0.001 (48)	0.6821 ± 0.0222
Gibbs 1991/1[b]	60/57								24/90			<0.001 (147)	0.3527 ± 0.0069
Gibbs 1991/2[b]	10/30								24/90			0.073 (120)	−0.1652 ± 0.0085
Gibbs 1991/3[b]	23/57								10/90			0.036 (147)	0.1748 ± 0.0069
Gibbs 1991/4[b]	10/30								10/90			1.000 (120)	0.0000 ± 0.0085
Møller 1989/1[b]	77/60	85/60					28/60					<0.001 (180)	0.3163 ± 0.0056
Møller 1989/2[b]	40/60	40/60					30/60					0.417 (180)	0.0606 ± 0.0056
Møller 1989/3[b]	77/60	75/60			55/60							0.019 (180)	0.1767 ± 0.0056
Møller 1989/4[b]	40/60	47/60			25/60							0.039 (180)	0.1551 ± 0.0056
Pasitschniak-Arts & Messier 1995	72/75			55/75		51/75						0.014 (225)	0.1653 ± 0.0045
Pasitschniak-Arts & Messier 1996	91/120			83/120		93/120						0.038 (360)	−0.1098 ± 0.0028
Picman et al. 1993		48/27			31/26							0.194 (53)	0.1803 ± 0.0200
Ratti & Reese 1988/1[b]	13/30	10/30	3/30	0/30	7/30 0/30							0.057 (180)	0.1429 ± 0.0056
Ratti & Reese 1988/2[b]	7/30	24/29	13/30 10/30	20/30	17/29	7/30						0.337 (208)	0.0667 ± 0.0049
Ratti & Reese 1988/3[b]	40/30	57/30	47/30		63/30 30/30 53/30							0.113 (180)	−0.1188 ± 0.0056
Ratti & Reese 1988/4[b]	17/29	44/37	64/28 77/26	71/28 65/26		67/27						<0.001 (201)	−0.3064 ± 0.0053

continued

Table 2. (continued)

Reference[a]	\	\	\	Distance from edge (m)	\	\	\	\	\	\	\	p (m)[e]	Zr ± CI[f]
	0	25	50	75	100	150	200	300	500	900	>1000		
Söderström et al. 1998/1[b]	47/38	27/38	34/38									0.465 (114)	0.0685 ± 0.0090
Söderström et al. 1998/2	71/38	71/38	61/38									0.532 (114)	0.0586 ± 0.0090
Storch 1991[b]	45/45		68/45		75/45							0.003 (135)	−0.2613 ± 0.0076
Wilcove et al. 1986/1[b]	29/24							20/20	15/20	15/20		0.612 (84)	0.0554 ± 0.0123
Wilcove et al. 1986/2[b]	95/20								45/20			<0.001 (40)	0.7744 ± 0.0270
Wilcove et al. 1986/3[b]	100/20								60/20			<0.001 (40)	0.7744 ± 0.0270
Natural nests													
Berg 1992/1		43/14	44/70									0.922 (84)	−0.0107 ± 0.0123
Berg 1992/2				37/30	48/54							0.308 (84)	−0.1117 ± 0.0123
Berg 1992/3				60/20	39/71							0.103 (91)	0.1727 ± 0.0114
Berg 1996/2			19/16				26/19					0.593 (35)	−0.0905 ± 0.0313
Berg 1996/3			17/6				9/155					0.564 (161)	0.0454 ± 0.0063
Best 1978[b]		90/85	82/22	96/16	83/8							0.442 (135)	−0.0663 ± 0.0076
Chasko & Gates 1982/1[b]	51/51	37/54	30/54	31/51		100/4						0.116 (210)	0.1091 ± 0.0049
Chasko & Gates 1982/2[b]	33/43	41/44	12/49									0.004 (136)	0.2520 ± 0.0075
Gates & Gysel 1978[d]	27/378		20/127		11/56							<0.001 (561)	0.1751 ± 0.0018
Honza et al. 1998[d]	18/57 30/43 20/30 26/23											0.478 (153)	−0.0574 ± 0.0067
Kristiansen 1998			79/14		67/6	0/4	0/7					<0.001 (31)	0.9454 ± 0.0357
Pasitschniak-Arts et al. 1998/1	77/13	100/8	80/10	77/13 100/2 100/3 75/4								<0.001 (53)	0.6390 ± 0.0200
Pasitschniak-Arts et al. 1998/2	75/8	53/17	50/4	80/5 33/6 20/5								0.196 (50)	0.1850 ± 0.0213
Pasitschniak-Arts et al. 1998/3	70/33	48/27	69/16	78/9 33/3 75/4 0/1 33/3								0.285 (96)	0.1013 ± 0.0092
Temple & Cary 1988[b]					82/96	42/98	30/82	50/4 50/2				<0.001 (276)	0.2524 ± 0.0037
Vickery et al. 1992[b]		33/6		70/12	56/13	40/8	87/8 75/5					0.405 (60)	−0.1079 ± 0.0175
Yahner 1991[b]	60/37	50/36	41/22									0.260 (95)	0.1161 ± 0.0109

[a]*Numbering after the year of the citation refers to different experiments from the same paper.*
[b]*Experiments from Paton (1994).*
[c]*NA, not available.*
[d]*Distances from the edge were 1, 2, 3, and >3 m.*
[e]*The p value is the significance of likelihood-ratio chi-square test; n is the number of nests.*
[f]*The Zr ± CI is the Fisher's z transformed, which is an effect size, and its 95% confidence intervals. Positive Zr indicates higher nest predation in the edge than in the interior habitats. If the confidence interval brackets zero, then edge effect is not significant at p = 0.05.*
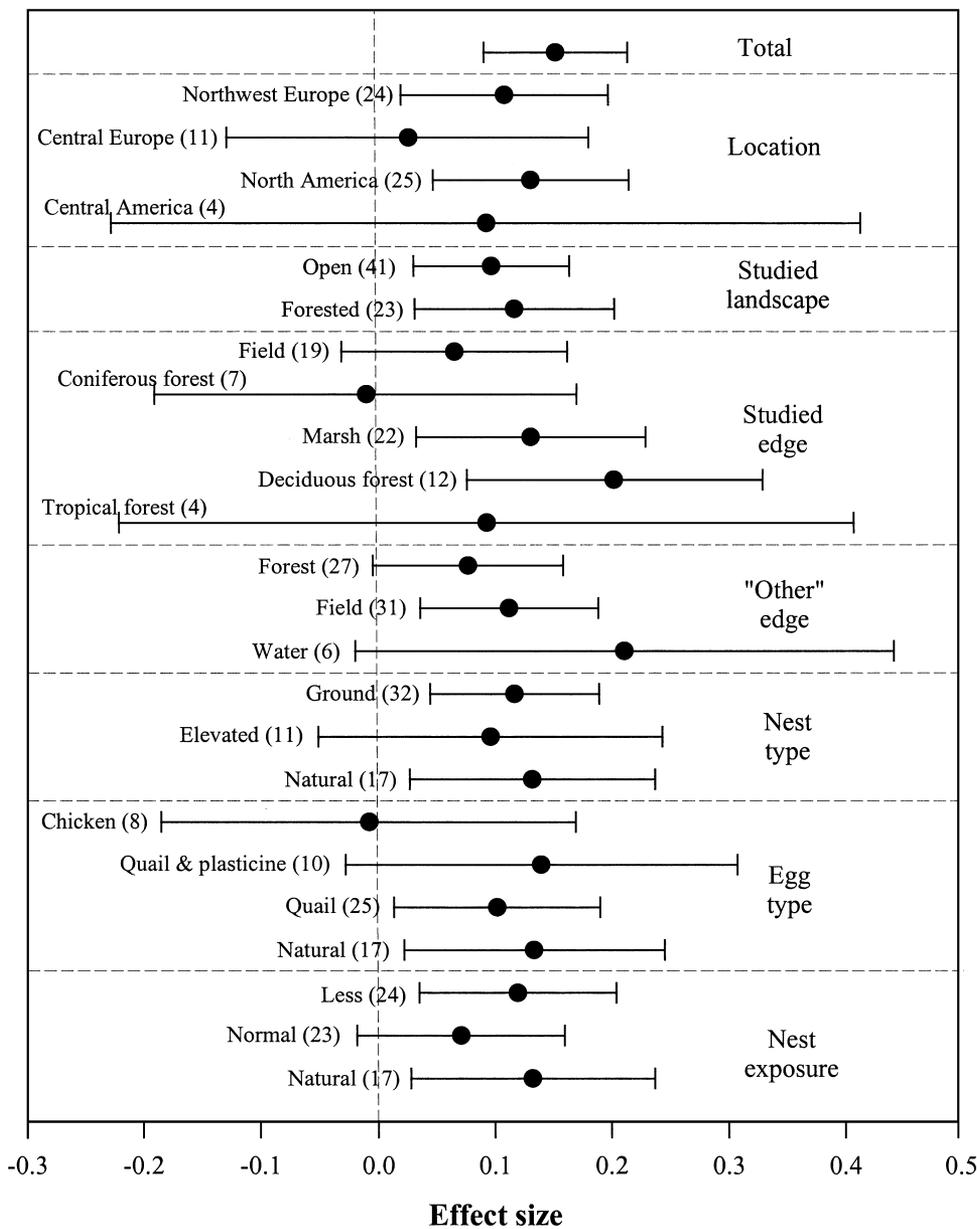
Figure 1. Effect sizes with 95% confidence interval (CI) of 64 evaluated experiments on nest-predation edge effect and of different groups of the experiments. Edge effect is significant at α = 0.05 if confidence intervals do not bracket zero. Number of experiments are given in parentheses. For example, the effect size for field as the studied edge is 0.0665, and the confidence limits are −0.0305 to 0.1635. This indicates a positive edge effect, but it is not significant at α = 0.05. Edge effect is significant for, for example, marsh and deciduous forests as studied edges. Grouping is based on the geographical location (location), landscape type of the studied edge (studied landscape), habitat type of the studied edge (studied edge), habitat type of the adjoining edge (other edge), nest type (nest type), egg type (egg type), and duration of exposure (nest exposure).

Lahti (2001) evaluated 55 studies and found no support for increased nest-predation rates near habitat edges. He did not use any statistics, however, so his qualitative results should be treated as his opinion. Chalfoun et al. (2002) recently investigated the mechanisms underlying fragmentation and edge effects and found that the response of nest predators to fragmentation is complex, taxon-specific, and context-dependent.

Although our review is the most comprehensive to date, there are some limitations to our results. Our results are seriously biased toward northern temperate regions. More needs to be learned about the impact of edge effects on avian nest success in tropical or southern temperate regions. Regarding the large differences in edge effect between tropical and temperate bird communities (Báldi 1996; Martin et al. 2000), the comparison of edge effect

may reveal basic ecological and biogeographical patterns in bird communities. From a practical conservation point of view, this geographical bias toward developed regions may be useful for habitat restoration plans. It would be desirable, however, to initiate future research in less developed areas to better understand nest-predation edge effects and to provide guidance to area managers in tropical regions threatened with increased fragmentation. We found considerable variation across habitats, nest and egg type, and exposure time. This inconsistency was the main cause of the lack of clear pattern (Paton 1994) and for the call to increase the number of studies examined (Hartley & Hunter 1998). This variability in experimental design is partly a result of the different model species and landscapes. For example, some investigators did not place artificial nests at the edge (0 m) because the modeled
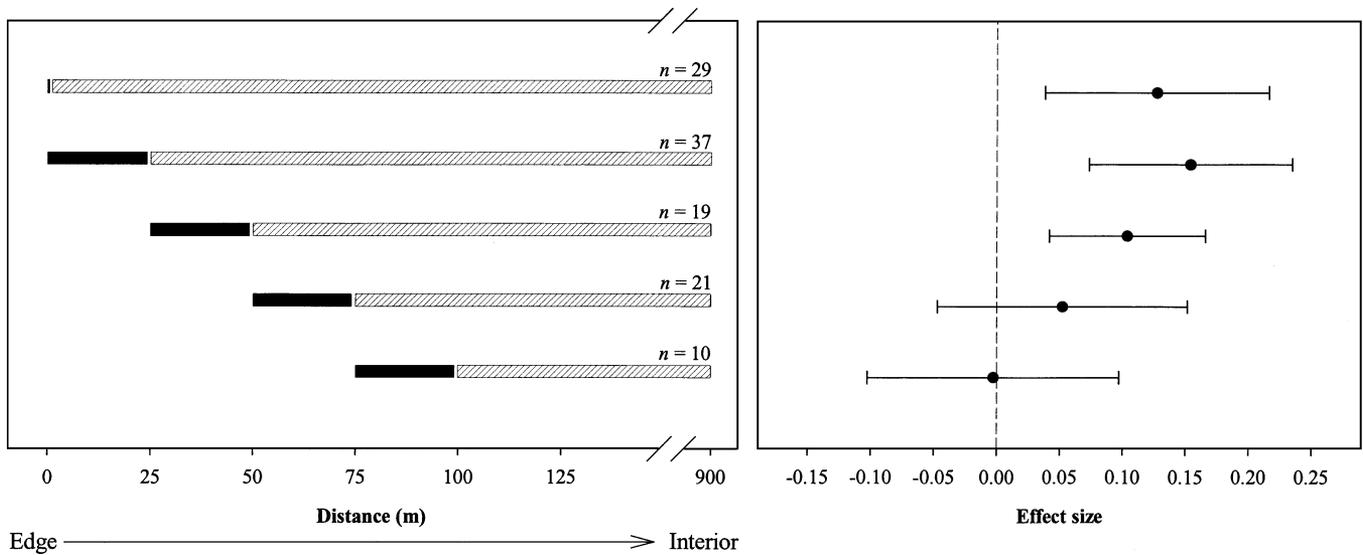
Figure 2. Distance of nest-placement range from the edge toward the interior, and effect sizes with 95% confidence interval (CI). The first row (top) shows experiments in which nests were placed on the edge (0 m) and farther inside (1–900 m) and the corresponding effect size with 95% CI. The second row includes experiments in which nests were placed within the first 24 m and farther inside (25–900 m), and so forth. Therefore, in the former case edge is only the 0-m belt; in the latter case the 0- to 24- m belt, then the 25- to 50- m belt, and so forth. Edge effect is significant at α = 0.05 if CI does not contain zero. The n *is the number of experiments.*

species (e.g., the Curlew [*Numenius tenuirostris*], Berg et al. 1992; Berg 1996) does not nest near forest. Therefore, we believe that the diversity of experimental designs was sufficient, but the number of experiments in less studied regions should be increased. For example, our own experiments represent the majority of central European experiments (9 out of 11). This may bias the results, thus pointing to the need for more experiments. In addition, the "edge" should be defined more accurately or quantified by some environmental factors such as light; vegetation height, density, and diversity; availability of potential

edge predators; and other factors in order to provide a more comprehensive understanding of the edge effect across habitat types and geographic areas (Paton 1994).

Debate is continuous on the reliability of artificial nest studies. The depredation of artificial nests usually differs from that of real nests (e.g., Willebrand & Marcstrom 1988; Buler & Hamilton 2000), so artificial nests should not be used to measure actual rates of nest predation (Wilson et al. 1998). However, they may be valuable for detecting trends in rates of predation (Major & Kendal 1996; Wilson et al. 1998).

Are there alternative hypotheses to explain heterogeneity in nest predation across edges? The first alternative hypothesis relates to landscape pattern (Andrén 1994, 1995). Several researchers have found that nest losses are correlated with forest cover, and increased nest predation in habitat edges was detectable only in fragmented landscapes (Robinson et al. 1995; Donovan et al. 1997; Hartley & Hunter 1998). Paton (1994) showed a positive relationship between patch size and nest success. Therefore, nest predation depends on landscape structure and not on the edge per se. An alternative hypothesis is that nest-predation edge effect is related to human influence on the landscape (Wilcove 1985). In this scenario, forest cover is an indicator of human habitat conversion and edge effect is related to the influence of human-dominated matrix in the landscape.

The edge-effect, landscape-structure, and human-influence hypotheses of nest predation are interrelated. To separate their effects, nest-predation experiments should
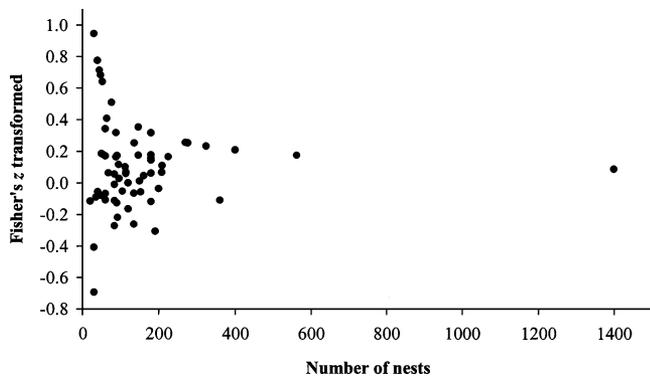

Figure 3. Funnel plot of the 64 nest-predation edge-effect experiments. The Fisher's z transformed is an effect size. The funnel shape indicates publication bias did not occur in the primary literature we analyzed.

be placed in a landscape context, which is a recently emerging desirable occurrence in field experiments (e.g., Donovan et al. 1997; Boulet et al. 2000). The comparison of naturally patchy and human-fragmented landscapes may reveal differences between the landscape-structure and the human-influence hypotheses.

Acknowledgments

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