Review

The Effect of Edge on Avian Nest Success: How Strong Is the Evidence?

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Abstract: *Wildlife biologists historically considered the edge between adjacent habitat types highly productive and beneficial to wildlife. A current dogma is that edges adversely affect a wide range of avian species by increasing depredation and parasitism rates of nests. I critically evaluated existing empirical evidence to test whether there was a gradation in nest success as a function of distance from an edge. Researchers investigating this question have been inconsistent in their experimental designs, making generalizations about edge-effect patterns difficult. The majority of studies I examined found nest success varied near edges, with both depredation rates (10 of 14 artificial nest studies, and 4 of 7 natural nest studies) and parasitism rates (3 of 5 studies) increasing near edges. In addition, there was a positive relationship between nest success and patch size (8 of 8 studies). The most conclusive studies suggest that edge effects usually occur within 50 m of an edge, whereas studies proposing that increased depredation rates extend farther than 50 m from an edge are less convincing. Prior research has probably focused on distances too far from an edge to detect threshold values, and future research should emphasize smaller scales: 100–200 m from an edge at 20–25 m increments. Researchers often use relatively arbitrary habitat characteristics to define an edge. Therefore, I propose that only openings in the forest canopy with a diameter three times or more the height of the adjacent trees should be included in edge analyses. This review suggests that fragmentation of eastern North American temperate forests could lead to increased nest predation and parasitism, and there is need to determine if similar processes occur in other forested regions of North America.*

El efecto de borde sobre el éxito en la nidificación: ¿Cuan firme es la evidencia?

Resumen: *Históricamente, los biólogos de fauna silvestre consideraron a los bordes entre tipos de habitats adyacentes como altamente productivos y beneficiosos para la fauna silvestre. Un dogma actual sostiene que los bordes afectan adversamente a un amplio rango de especies de aves al incrementar las tasas de predación y parasitismo de los nidos. Yo evalué críticamente la evidencia empírica existente para establecer si existía un gradiente en el éxito de los nidos en función de la distancia a un borde. Los investigadores que analizaron esta cuestión han sido inconsistentes en el diseño de sus experimentos, haciendo difícil las generalizaciones acerca de los patrones del efecto de bordes. La mayoría de los estudios que examiné establecieron que el éxito de los nidos varió cerca de los bordes, observandose un incremento tanto en las tasas de predación (10 de 14 estudios de nidos artificiales y 4 de 7 estudios de nidos naturales) como de parasitismo (3 de 5 estudios) cerca de los bordes. Además existió una relación positiva entre el éxito de los nidos y el tamaño de los parches (8 de los 8 estudios). Los estudios más decisivos sugieren que los efectos de borde ocurren usualmente a menos de 50 m del borde, mientras que los estudios que proponían que los incrementos en las tasas de predación se extendían más allá de 50 m del borde fueron poco convincentes. Investigaciones anteriores se concentraron, posiblemente, en distancias muy alejadas del borde como para detectar valores de umbral y la investigación futura debería enfatizar menores escalas; 100–200 m del borde con incrementos de 20–25 m. Los investigadores usan frecuentemente características del hábitat relativamente arbitrarias para definir un borde. Por consiguiente propongo que sólo se incluyan en los análisis de borde aberturas en el canopeo forestal que posean un diámetro su-*

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perior a 3 veces la altura de los árboles adjacentes. Esta revisión sugiere que la fragmentación de las forestas del este de Norte América podría conducir a un incremento en la predación y parasitismo de nidos, y que es necesario determinar si procesos similares ocurren en otras regiones forestales de Norte América.

Introduction

Many biologists consider the edge between adjacent habitat types a positive feature of the landscape for wildlife (see Kremsater & Bunnell 1992). This belief is based in part on Leopold's (1933) "law of interspersion," which postulated that increases in the amount of edge habitat resulted in higher population densities (Guthery & Bingham 1992). Leopold's edge-effects hypothesis led many wildlife biologists to create edges to enhance habitat for game species (for example, Yoakum et al. 1980: 402). Within the past decade, however, wildlife biologists have pointed out that Leopold's hypothesis pertained only to certain species and have challenged the idea that edges benefit most wildlife (see Reese & Ratti 1988; Yahner 1988).

Much of the recent interest in edge is due to avian population declines in fragmented landscapes, as exemplified by neotropical migrants in eastern North America (Askins et al. 1990; Hagan & Johnston 1992). In a recent summary of breeding season mortality factors for 32 species of neotropical migrants, Martin (1992) identified nest predation as the most important cause of nest failure. Therefore, determining what factors influence nest predation is imperative if biologists hope to successfully manage many avian populations.

One of the most frequently cited explanations for population declines in fragmented landscapes is higher nest depredation rates near edges, hereafter referred to as edge effects. Gates and Gysel (1978) developed the "ecological trap" hypothesis, which postulated that nest predation rates were density-dependent, with greater nest densities and a concomitant increase in depredation rates near edges. Subsequent studies have refuted this hypothesis, however, based on data with artificial nests showing that nest success did not decline near edges (Angelstam 1986; Ratti & Reese 1988).

Because the data are equivocal, I was interested in the circumstances when edge effects appear to be an important biological phenomenon. My purpose is to (1) summarize existing literature that quantified the relationship between nest loss (either by predation or parasitism) and distance from an edge (or patch size), (2) re-analyze these data where possible, (3) summarize the conditions when predation and parasitism rates change near edges (for example, degree of contrast between adjoining habitats, forested versus unforested habitats, type of predator), and, finally, (4) discuss what conclusions I believe realistically can be drawn from existing empirical evidence.

Methods

I have divided this review into two sections. The first section, on distance as an independent variable, deals with studies that used artificial or natural nests to quantify the relationship between nest success and distance from an edge. I attempted to include in this review all studies that have directly measured nest success as a function of distance from an edge. The second section, on patch size as an independent variable, analyzes studies that indirectly investigated edge effects by quantifying the relationship between nest success and patch size. There is a large body of literature focusing on the relationship between patch size and avian species richness (for example, Lovejoy et al. 1986; Hagan & Johnston 1992), but there are fewer published papers that have quantified the relationship between patch size and nest success.

Study-site habitat types ranged from tropical forests in Central America (one study), coniferous forests in western North America (two studies), deciduous forests in eastern North America (five studies), and a mixture of habitat types in Europe (six studies; Table 1). Because nests were placed across a broad spectrum of different habitat types, they were exposed to a variety of potential predators (Table 1). Five of the studies (Yahner & Wright 1985; Angelstam 1986; Andrén & Angelstam 1988; Møller 1989; Yahner 1991) found that corvids were the primary predators at their study sites, whereas red squirrels (*Tamiasciurus hudsonicus*) were in Alberta (Boag et al. 1984), skunks (*Mephitis mephitis*) were in Maine (Vickery et al. 1992), and snakes were in grasslands of Illinois (Best 1978). The other studies did not identify a principal predator.

I tested whether nest success was independent of either distance from an edge or of patch size using a likelihood-ratio chi square (G) test (Agresti 1990). Many of the studies presented here originally used a likelihood-ratio test to analyze their data (Yahner & Wright 1985; Møller 1988, 1989; Berg et al. 1992). Each nest was considered an independent observation (although see below for a discussion of Gates & Gysel [1978] and Chasko & Gates [1982]). I considered p values <0.1 significant, as I wanted to be statistically conservative to minimize Type II errors (concluding there was no evidence for edge effects, when in fact they existed) and was not as concerned with Type I errors (concluding edge effects exist when they do not).

Most artificial nests studies reviewed here used either real chicken or quail (*Coturnix coturnix*) eggs, with

Table 1. Summary of primary predators and methods used in nest predation studies.

Reference	*Location*	*Primary Predators*[a]	*Type of Nest*[b]	*Type of Eggs (n)*[c]	*Exposure Days*
Artificial Nests					
Andrén & Angelstam 1988	Sweden	C[1] RF PM	OG	C (2)	8
Angelstam 1986	Sweden	C[1] RF PM	OG	C (2)	14
Avery et al. 1989	Scotland	ST RF C[2]	OG	C (1)	8
Berg et al. 1992	Sweden	ND	OG	Q (2)	28
Boag et al. 1989	Alberta	RS DM C[3]	OG	Q (5–7)	22
Burger 1988	Missouri	C[4] M[1]	W-CG	Q (1–3)	7
Carlson 1989	Missouri	ND	CG	Q (1)	7
Gibbs 1991	Costa Rica	M[2] B SN	W-OG/OE	Q (1)	7
Møller 1989	Denmark	C[5]	OG/CG	P (3)	7
Ratti and Reese 1988	Idaho	C[6] CH RS	W-OG/OE	Q (2)	12
Wilcove et al. 1986	Maryland	CH C[7] RF	W-OG	Q (3)	7–25
Small & Hunter 1988	Maine	RF RS SS	W-OG	C (3)	8
Storch 1991	W. Germany	M C[8]	OG	C (3)	35
Yahner & Wright 1985	Pennsylvania	C[4] R RF	OG	C (3)	6
Natural Nests					
Best 1978	Illinois	SN			
Chasko & Gates 1982	Maryland	CH RF C[7]			
Gates & Gysel 1978	Michigan	C[7] CH M B			
Yahner 1991	Pennsylvania	C[4]			
Vickery et al. 1991	Maine	SS			

[a] *B = birds, C = corvids* ([1]Corvus corax, C. cornix, C. monedula, Pica pica; [2]C. cornix; [3]Perisoreus canadensis; [4]C. brachyrhynchos; [5]C. cornix, P. pica, Garrulus glandarius; [6]Cyanocitta stelleri, P. c., C. corax, C. b.; [7]Cyanocitta cristata, C. b.; [8]C. corax, C. corone, G. g., Nucifraga caryocatactes), *CH = chimpmunk* (Tamais *spp.*), *DM = deer mouse* (Peromyscus maniculatus), *M = mammals* ([1]Didelphis virginiana, Procyon lotor, Mephitis mephitis, Sciurus carolinensis; [2]Nasua narica, Mustela frenata, Eira barbara, Potos flavus, Sciurus granatensis, Tayassu tajacu, [3]*PM, RF, RS,* Meles meles, Mustela nivalis), *ND = no data, PM = Pine Marten* (Martes martes), *R = red fox* (Vulpes vulpes), *RS = red squirrel* (Tamiasciurus hudsonicus), *SN = snakes, SS = striped skunk* (Mephitis mephitis), *ST = stoat* (Mustela erminea).

[b] *CG = covered, on ground, OE = open, elevated (1–3 m high), OG = open, on ground, W = in wicker basket.*

[c] *C = chicken, P = plasticine, Q = quail* (Coturnix coturnix).

clutch sizes ranging from one to seven eggs (Table 1). The only exception was Møller (1989), who used plasticine eggs to determine the species of corvid predators preying on nests based on bill markings on the artificial eggs. The majority of artificial nest studies exposed eggs to predators for 6–8 days (8 of 14; 57%) and used open, ground nests. This type of nest generally experiences the highest depredation rates (Ratti & Reese 1988; Gibbs 1991; Martin 1992; but see Yahner et al. 1989). For example, Møller (1989) observed that open nests were depredated at a higher rate than partially covered nests, 64% versus 36% respectively.

Distance as an Independent Variable

Predation Rates of Artificial Nests

I re-analyzed data from 14 studies, subdivided into 33 "treatments," that used artificial bird nests to investigate the relationship between distance from an edge and nest success (Table 2). Table 2 emphasizes the inconsistencies in the experimental designs of these studies. The large variance in the distance increments among the 14 studies makes it extremely difficult to ascertain anything conclusive about edge-effect patterns. Only one study, Ratti and Reese (1988), spaced nests at equidistant intervals to adequately determine where threshold values might occur (Table 2). Some studies did not place any artificial nests near the edge (≤50 m; Avery et al. 1986; Berg et al. 1992), others spaced nests relatively far apart (>300 m; Wilcove et al. 1986; Angelstam 1988; Gibbs 1991), several studied nests 1000 m or more from an edge (Angelstam 1986; Wilcove et al. 1986; Avery et al. 1989), and others placed nests only 50 m or less from an edge (Boag et al. 1984; Yahner & Wright 1985).

Notwithstanding this tremendous variation in experimental designs, a majority of the studies (10 of 14; 71%) had at least one treatment that found significant variation in nest success near an edge (Table 2). I next tested whether treatments conformed to Gates and Gysel's (1978) hypothesis that nest success decreased near edges and found most studies supported their hypothesis. Based on 19 treatments that found differential nest success near an edge, 15 had poorer nest success near an edge ($X^2 = 3.5$, d.f. $= 1$, $p = 0.062$; Table 2). One interesting exception was Storch (1991), who found that artificial nest success decreased farther from the edge and that Capercaillie (*Tetrao urogallus*) selected nest sites near the edge (<25 m), suggesting that the increased cover near the edge provided refuge from nest predators.

Based on my review of these studies, at least four generalizations concerning landscape patterns can be made. First, although more studies are needed with nests located nearer to edges, these data suggest that nest predation rates are greatest at less than 50 m from

Table 2. Studies investigating depredation rates of avian nests (% nest loss) as a function of distance from an edge.[*]

Distance from edge (m)													Type of	
0	*25*	*50*	*75*	*100*	*200*	*300*	*500*	*1000*	*1500*	*>1500*	*P*[a]	*N*[b]	*edge*[c]	*References*
Artificial Nests														
50		61		54		61					0.836	92	FA-CF	Andrén & Angelstam 1988
50		33		13			8				0.004	88	CF-FA	Andrén & Angelstam 1988
		67			59			70	60	61	0.885	150	CF-FA	Angelstam 1986
				44			37	33	30		<0.001	1512	MO-CF	Avery et al. 1989
		61				58					0.790	96	BO-WO	Berg et al. 1992
		38				7					0.002	64	BO-WO	Berg et al. 1992
		58				64					0.723	40	BO-WO	Berg et al. 1992
		35				61					0.015[f]	84	BO-WO	Berg et al. 1992
		20				9					0.057	88	BO-WO	Berg et al. 1992
		15				10					0.604	68	BO-WO	Berg et al. 1992
58	70										0.232	90	DF-TR	Boag et al. 1984
	65	37									<0.001	324	DF-FI	Burger 1988:30
		30	11								<0.001	270	PR-WO	Burger 1988:49
95					34	23	24				<0.001	400	DF-FI	Carlson 1989
		72		64	76	72					0.611	200	DF-FI	Carlson 1989
60							24				<0.001	147	TF-SG	Gibbs 1991[d]
10							24				0.073[f]	120	TF-FA	Gibbs 1991[d]
23							10				0.036	147	TF-SG	Gibbs 1991[e]
10							10				1.000	120	TF-FA	Gibbs 1991[e]
77	85				28						<0.001	180	FI-CF	Møller 1989[g]
40	40				30						0.417	180	FI-CF	Møller 1989[h]
77	75			55							0.019	180	CF-FI	Møller 1989[g]
40	47			25							0.039	180	CF-FI	Møller 1989[h]
	40	57	47	63	30	53					0.113	180	CF-FI	Ratti and Reese 1988[i]
17	44	64	77	71	65	67					<0.001[f]	191	CF-FI	Ratti and Reese 1988[j]
	13	10	3	0	7	0					0.057	180	FI-CF	Ratti and Reese 1988[i]
7	24	13	10	20	17	7					0.337	208	FI-CF	Ratti and Reese 1988[j]
											>0.100	508	CF-UK	Small and Hunter 1988[k]
45		68		75							0.003[f]	135	CF-CC	Storch 1991
29						20	15	15			0.612	84	DF-FI	Wilcove et al. 1986[l]
95							45				<0.001	40	DF-FI	Wilcove et al. 1986[m]
100							60				<0.001	40	DF-FI	Wilcove et al. 1986[n]
55[k]		55[k]									>0.360	384	DF-CC	Yahner and Wright 1985
Natural Nests														
90		82	96	83	100						0.442	135	PR-WO	Best 1978[o]
51	37	30	31								0.116	209	DF-CC	Chasko and Gates 1982[p]
33		41	12								0.004	136	DF-CC	Chasko and Gates 1982[p]
	27	20		11							<0.001	562	DF-FI	Gates and Gysel 1978[p]

Table 2. Continued.

Distance from edge (m)													Type of	
0	25	50	75	100	200	300	500	1000	1500	>1500	P[a]	N[b]	edge[c]	References
											<0.100	350	PR-WO	Johnson & Temple 1990[k]
		82		42	30						<0.001	276	DF-FI	Temple and Cary 1988
60	50	41									0.26	95	DF-CC	Yahner 1991
	33		67	62	38	88	75	50	50		0.40	60	GR-DF	Vickery et al. 1992

* P *values are based on re-analysis for this summary and may differ from original published values.*

[a] *Likelihood ratios (G^2) testing whether nest fate was independent of distance from edge.*

[b] *Total number of nests.*

[c] *Nests were located in boldface habitat: CF = conifer forest, CC = clearcut, DF = Deciduous forest, FI = Field, FA = Farmland, GR = grassland, MO = moorland, OG = old-growth forest, PR = prairie, TF = tropical forest, TR = Trail, UK = unknown, WO = woodland.*

[d] *Ground nest.*

[e] *Elevated nests.*

[f] *Nest loss was greater farther from edge.*

[g] *Open ground nests.*

[h] *Covered ground nests.*

[i] *Abrupt edge.*

[j] *Feathered edge.*

[k] *Exact predation rates not given; only* P *values were presented.*

[l] *7-d experiment.*

[m] *14-d experiment.*

[n] *25-d experiment.*

[o] *Based on my analysis of Best 1978, Fig. 4.*

[p] *% loss calculated for each egg, not for each nest.*

an edge, based on three lines of evidence. Only within 25 m of an edge was there more than 80% nest loss (Table 2). Studies that did not have nests located less than 50 m and more than 50 m from an edge often did not find evidence for edge effects (Boag et al. 1984; Yahner & Wright 1985; three of six treatments by Berg et al. 1992). Finally, the only two studies that had nests spaced relatively close together found that edge effects occurred less than 50 m from an edge (Burger 1988; Ratti & Reese 1988).

Other studies that found support for edge effects were more difficult to interpret. For example, Wilcove et al. (1986:251) inferred a linear decline in depredation rates up to 600 m from an edge and suggested edge effects could extend from 300 to 600 m into the forest. Yet my re-analysis of his data found that only nests exposed for 14 and 25 days at 0 and 600 m from an edge showed statistically significant evidence for edge effects (Table 2). There is no reason to believe this was a linear relationship, however, and a threshold value could occur anywhere from 0 to 600 m from the edge. A similar dilemma occurs with data gathered by Møller (1989), Gibbs (1991), and Berg et al. (1992), as their nests were distributed 100 m or more apart.

A second generalization is that significant edge effects were as likely to occur in unforested habitats (7 of 13 treatments) as in forested habitats (13 of 20 treatments) ($G = 0.41, p > 0.5$; Table 2). Third, depredation rates in northern conifer forests appear to be greater in forested habitats than in adjacent unforested habitat (Andrén & Angelstam 1988; Ratti & Reese 1988), although work by Møller (1989) did not support this idea. This may be because corvids are among the primary nest predators in boreal forests, and unforested habitat lacks perches used by many avian predators for nest searching (Ratti & Reese 1988).

Current biotic studies are inconclusive concerning the influence of the type of edge on edge effects. Ratti and Reese (1988) studied plots with an abrupt edge and a "feathered edge" (that is, a shelterwood timber removal). They found predation rates were greater on either side of a feathered edge compared to an abrupt edge, although predation rates within the feathered edge were relatively low. In contrast, Yahner et al. (1989) found no variation in nest success based on edge contrast.

Although my re-analysis of 10 of the 14 studies found statistical support for edge effects, at least one study (Avery et al. 1986) probably had no biological significance. This was due to minimal variation in nest success (30–44%) coupled with a large sample size (Table 2). Also, once Avery et al. (1986) factored out vegetational differences, they found no evidence to support edge effects. I found two significant relationships in the data of Ratti and Reese (1988), where they reported none. One discrepancy was due to the conservative p value I used, and the other was their feathered-edge forest plot, where I included an edge datum (17%) in my computations and they excluded it.

It is my opinion that three of four studies that found no evidence for edge effects were dubious tests of any edge effects hypothesis. Two studies (Boag et al. 1984;

Yahner & Wright 1985) did not place nests far enough away from an edge; that is, their artificial nests were potentially located within a relatively homogeneous band of high predation pressure, and predation rates might have declined beyond the area they sampled. Boag et al. (1984) compared predation rates only for nests less than 15 m to those greater than 20 m from a trail. Yahner and Wright (1985) placed nests at 0 m and 50 m from the edge of 1-ha forest fragments, in stands they concluded were composed entirely of edge habitat.

Another type of problem was the relatively arbitrary definition many researchers used to define an edge. Angelstam (1986) placed nests 20–40 m from roadsides at 500 m intervals yet assumed that nests were located as far as 1.5 km from the forest-farmland edge. I believe Angelstam's (1986) data might have been more properly classified as less than 50 m from an edge, because nests were placed near a road. This is especially true because corvids often follow roads to look for potential prey, and 75% of the nests in this study were taken by corvids (Angelstam 1986:367). The fourth study that found no evidence for edge effects, Small and Hunter (1988), did not present their data in a format conducive to re-analysis.

Ratti and Reese (1988) had a rigorous experimental design with one potential problem. They had two study plots, 2.4 ha and 6.2 ha, which were both small enough to be within the confines of a corvid territory. A different experimental design, which used a larger number of study plots and increased the distance between artificial nests, would reduce the probability that a minimal number of predators were responsible for all depredations (see Laurance & Yensen [1991] for further discussion).

Predation Rates of Natural Nests

Four of the seven studies (57%) that examined natural nest success had at least one significant treatment supporting the existence of edge effects (Table 2). In contrast to artificial nest experiments, natural nests were usually not studied farther than 100 m from an edge, with the exception of the studies by Temple and Cary (1988) and Vickery et al. (1992). Nevertheless, edge effects were still found at this relatively small scale, again suggesting that edge effects generally occur close to edges.

Johnson and Temple (1990) had two distance categories, less than 45 m or 45 m or more, and they found that nests near an edge had higher depredation rates. Their data presentation precluded further analyses, however, because nest success was based on exposure days rather than apparent nest success. Best (1978: Figure 4) did not directly analyze edge effects, but I estimated edge effects based on his sketch of the location of nests. Predation pressure was very high at his shrub-grassland study area, with 76% of all nests lost to snakes (Best 1978). Failed nests were evenly distributed throughout his study area. Vickery et al. (1992) did not find any evidence for edge effects in grasslands where striped skunks were the principal predator. In fact, nest success was greatest at less than 50 m from the woodland edge, although this relationship was not statistically significant.

Gates and Gysel (1978) and Chasko and Gates (1982) found a positive relationship between nest hatching success and distance from the edge. However, data from both studies should be interpreted with caution. They presented predation rate information for each egg rather than for individual nests (J. E. Gates, personnel communication), making re-analysis of their data impossible. For example, Gates and Gysel (1978:876) calculated fledging success based on 562 eggs rather than 194 nests. Individual nests were the independent sampling unit, because once one egg was taken from a nest, the probability increases that all eggs in the nest will be preyed on.

Parasitism Rates of Natural Nests

Three of five studies concluded that parasitism rates of Brown-headed Cowbirds (*Molothrus ater*) declined away from edges (Table 3). Gates and Gysel's (1978) data suggested a similar relationship, but their trend was not significant.

Johnson and Temple (1990) found all five potential host species at their tallgrass prairie site were more likely to be parasitized by cowbirds when nests were less than 45 m from a wooded edge and in small fragments of prairie (<32 ha). Best (1978:18) studied nesting Field Sparrows (*Spizella pusilla*) in the shrub-grasslands of central Illinois and found that parasitized nests averaged 13.4 m from an adjacent woodland, whereas successful nests averaged 31.5 m from the edge. Brittingham and Temple (1983) worked in a 1000-ha deciduous forest in Wisconsin and found that cowbirds were much more likely to parasitize nests in open habitat (>40% open, forest canopy within 200 m of nests) compared to contiguous forested habitat (<20% open).

Further evidence suggesting that habitat fragmentation results in increased cowbird nest parasitism is provided by Robinson (1992), who worked in a fragmented landscape in Illinois and found that 76% of neotropical migrant nests were parasitized. In contrast, Sherry and Holmes (1992) have not documented any cowbird parasitism in over 20 years of research at their field site in an unfragmented forest in New Hampshire.

Patch Size as an Independent Variable

Predation of Artificial and Natural Nests

All eight studies I reviewed demonstrated a positive relationship between patch size and nest success, with the

Table 3. Summary of studies investigating cowbird parasitism rates (% nests parasitized) of natural avian nests as a function of distance from an edge.

Distance from edge (m) 0	25	50	75	100	200	300	500	1000	>1000	P[a]	N[b]	Habitat type[c]	References
		65		46	36	18				0.004	105	DF	Brittingham and Temple 1983[d]
17	5	0	0	0						0.013	171	PR	Best 1978[e]
		25	14							0.015	350	PR	Johnson and Temple 1990
7	0	19	6							0.216	62	DF	Chasko and Gates 1982
	15	8	14							0.445	40	DF	Chasko and Gates 1982
12	10	3	6							0.395	164	DF	Gates and Gysel 1978

[a] *Likelihood ratio (G^2) testing whether parasitism rates were independent of distance from an edge.*
[b] *Total number of nests.*
[c] *DF = deciduous forest, PR = prairie.*
[d] *Edge was considered any gap in the forest canopy ≥0.2 ha (not 0.02 ha in the paper, S. Temple, personal communication).*
[e] *Based on my analysis of Best 1978, Figure 4.*

exception of one treatment of Møller (1988) (Table 4). As with studies that investigated distance as an independent variable, there was a great deal of variation in the size spectrum and habitat types of patches, making generalizations difficult (Table 4). Burger (1988) tested for edge and area effects simultaneously and found that predation rates were more closely associated with distance from an edge. Much of the variation in depredation rates was probably due to variation in predator abundances associated with individual habitat patches (Table 1). For example, Wilcove (1985) found higher predation rates in urban forest fragments than in rural fragments, and Møller (1988) showed that predation rates increased regardless of patch size when a breeding pair of magpies (*Pica pica*) was present. For the most part, only patches less than 10 ha in size had relatively high depredation rates (≥50% nest predation rates; Table 4). If one assumes that edge effects occur 50 m or less from an edge,

Table 4. Summary of studies investigating depredation rates of avian nests (% nest loss) as a function of island size.

Island size (ha) <1	<5	10	25	50	100	200	300	1000	>1000	P[a]	N[b]	Forest type[c]	References
Artificial nests													
83	46	54	59	35			37			<0.001	324	DF	Burger 1988:28
		39	19	9	15		30			<0.001	270	PR	Burger 1988:50
		46				25				<0.001	250	TR	Gibbs 1991[d]
		33				13				<0.001	250	TR	Gibbs 1991[e]
										<0.100	350	PR	Johnson & Temple 1990[f]
83 78 72 44 55 44										0.040	108	DF	Møller 1988[g]
61 72 50 39 11 17										<0.001	108	DF	Møller 1988[h]
		31			19	7				<0.001	2684	DF	Telleria & Santos 1992
		33	66	16 11	12	27	9	3		<0.001	506	DF	Small & Hunter 1988
	71[i]48[j]						48	18	2	<0.001	360	DF	Wilcove 1985[k]
68	19	9								<0.001	420	DF	Yahner and Scott 1988
Natural nests													
100 60 50 44 32 31										0.031	89	DF	Møller 1988[g]
50 36 37 25 26 20										0.650	80	DF	Møller 1988[h]

[a] *Likelihood ratio (G^2) testing whether nest fate was independent of island size.*
[b] *Total number of nests.*
[c] *TR = tropical forest, DF = deciduous forest, CF = conifer forest.*
[d] *Ground nests.*
[e] *Elevated nests.*
[f] *Unable to re-analyze, only p value presented.*
[g] *Magpies absent.*
[h] *Magpies present.*
[i] *Mean for suburban woodlots.*
[j] *Mean for rural woodlots.*
[k] *Not all values for this study are included; see original reference.*

then an 10-ha patch would maintain 4.7 ha of core habitat with reduced predation pressure, whereas assuming 100-m-wide edge effects results in a core area of only 1.4 ha.

Discussion

Our current understanding of the biotic and abiotic effects of edges is still in its infancy (Laurance & Yensen 1991; Saunders et al. 1991; Bierregaard et al. 1992; Kremsater & Bunnell 1992). Much of the research on the potential changes in depredation rates near edges is based on work with artificial nests. Research with artificial nests should be interpreted with caution, however, because there is evidence to suggest that avian predators using visual cues are much more likely to prey on artificial nests, whereas mammalian predators using olfactory cues are primarily attracted to natural nests (Willebrand & Marcström 1988). Therefore, there may be a poor correlation between the predation rates of artificial nests and natural nests (see Reitsma et al. 1990), and studies using artificial nests may be biased towards predators using visual cues. In fact, when researchers were able to identify the principal predator, many studies I reviewed found that avian predators were responsible for the majority of artificial nest losses. However, artificial nests may provide an estimate of relative predation rates.

There are wide discrepancies in the vegetation characteristics researchers use to classify edges; therefore, there is a need to formalize the criteria used to include patches in edge analyses. For example, Boag et al. (1984) determined that man-made and game trails were wide enough to form edges in lodgepole pine (*Pinus contorta*) forests, whereas Angelstam et al. (1986) ignored edges created by roads in boreal forests and assumed edges were the nearest farmland patch. Burger (1988) used any woody vegetation to define edges at her prairie study site. Brittingham and Temple (1983) used 0.2-ha (45-m radius) openings in the forest canopy to define the source of edge habitat, as this patch size was the smallest they could detect from their aerial photos. This latter definition is purely a function of the scale of aerial photos, however, rather than a meaningful biological scale. Finally, many researchers neglect to provide readers with an accurate assessment of the landscape where the nest studies took place.

Using the forest canopy height to classify edges would be one way to eliminate ornithologists' past arbitrary criteria, because all studies I reviewed focused on the juxtaposition of forested (tropical, deciduous, coniferous) and unforested habitat (moorlands, fields, farmlands, clearcuts, prairies, grasslands). The silviculture literature suggests that the microclimatic conditions at the center of an opening with a diameter 2–3 times the height of the surrounding trees are similar to those of larger openings (Smith 1986:206). Therefore, researchers could include in edge analyses any opening in the forest canopy with a diameter three or more times the adjacent tree height, while smaller openings would be excluded. However, certain species, such as cowbirds, might perceive smaller openings as edges (Brittingham & Temple 1983). These same criteria could be used for unforested habitats (for example, prairies) with small woodlands, by ignoring woodlands with a diameter less than three times the mean tree height. Another approach would be for researchers to clearly state the biological reasons why a particular habitat feature is an edge to the organisms under investigation.

In addition, all the studies in this review focused on anthropogenic changes in the landscape, so called "induced" edges, even though there are also natural, long-lived, "inherent" edges (Yahner 1988). The biological distinctions between inherent and induced edges are relatively unexplored and need further research.

My review of the existing literature suggests that nest success declines near edges, but on a smaller scale than some authors have suggested (for example, Wilcove et al. 1986). The current evidence, although equivocal, suggests that predation and parasitism rates are often significantly greater within 50 m of an edge, and studies suggesting that edge effects occur beyond this potential threshold value are less convincing. This conclusion should be interpreted with caution, however, due to the lack of consistency in the experimental designs of these studies.

This leads to another important point. Research on abiotic and vegetational processes suggests that edge effects generally occur less than 50 m into a forest stand (Ranney et al. 1981; Kapos 1989; Laurance & Yensen 1991). Therefore, given this empirical evidence and the fact that my analyses suggest nest edge effects usually occur within 50 m of an edge, ornithologists should probably focus future edge research on a much smaller scale to quantify threshold values for depredation rates of artificial and natural nests. More data are needed within 100–200 m of the ecotone between forest and unforested habitat, and at smaller distance increments (about 20–25 m). Laurance and Yensen (1991) also provide some useful insights into study designs.

Two aspects of edge effects that have been relatively unexplored are the relationship between predator densities and nest success and how nest predators (or brood parasites) search for nests. Andrén (1992) found marked variation in the species of corvid predators using different habitat types in Sweden. Møller (1989) observed that Hooded Crows (*Corvus cornix*) wandered across habitat types, magpies concentrated their activities along the edge, and jays (*Garrulus glandarius*) were woodland specialists, indicating that knowledge of the autecology of nest predators in a particular habitat is vital to understanding potential depredation problems. Norman and Robertson (1975) reported that female cowbirds often remain motionless for hours searching for potential hosts nests; therefore, perches that provide a good view of surrounding habitat may be a critical habitat feature to female cowbirds. This is possibly why cowbirds usually only parasitized nests within 13 m of the woods-grassland ecotone (Best 1978). Normand and Robertson (1975) also reported that cowbirds actively search edge habitat trying to flush incubating birds.

Perches with a clear view of the surrounding habitat are probably also very important to nest predators (Ratti & Reese 1988; Møller 1989). Avery et al. (1989) found no biological evidence for edge effects when placing nests 100 m or more from the woodlands-ecotone. However, if avian predators use the woods for perch sites to locate nests in adjacent unforested habitat, 100 m might have been too far to find hidden artificial nests. The same argument holds true for Berg et al. (1992), and nests possibly should have been placed within 50 m of the woods to determine if edge effects occurred on a smaller scale.

Clearly strong evidence exists that avian nest success declines near edges. But more data are needed concerning potential threshold values for edge effects in a variety of landscape patterns and habitat types (Laurance & Yensen 1991). In North America, I found no studies that investigated edge effects in the forests of the southeastern or northwestern United States, even though these two areas are among the largest timber producers on the continent. Finally, future research should focus on realistic landscape scales with solid experimental designs to quantify the spatial extent of nest depredation and parasitism.

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