

# The “edge effect on nest predation” hypothesis after twenty years

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## Abstract

A majority of empirical tests have failed to support the hypothesis that avian nest predation increases near habitat edges. Of 54 study sites, 13 exhibited an edge effect in any test conducted, 31 did not exhibit one, and 10 exhibited an edge effect in at least one treatment but not in at least one other. Edge type has not generally been supported as an important factor in determining the existence of an edge effect. An edge effect has been exhibited slightly more often in landscapes of high fragmentation (< 50% prey habitat) than low (> 75% prey habitat), especially in forest. The few studies containing reliable predator identification have explained their results with species-specific predator behavior and its relation to habitat and landscape features. This may be a more fruitful approach to understanding nest predation dynamics than a focus on habitat edges per se. © 2001 Elsevier Science Ltd. All rights reserved.

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## 1. Introduction

Numerous studies of avian reproductive success, particularly among the Anseriformes, Galliformes, and Passeriformes, have concluded that the destruction of eggs and nestlings by predators is the most significant influence on nesting success (e.g. Hahn, 1937; Lack, 1954, p. 77; Nice, 1957; Ricklefs, 1969; Martin, 1992). Although Lack (1954, p. 154) concluded that mortality of adult birds was the primary influence on population numbers, Fretwell (1972) demonstrated that predation of eggs and nestlings could affect population density. Further work has suggested that variability in nest predation rate can be linked to subsequent population age structure (Sherry and Holmes, 1992), and may have played a role in the evolution of avian life-histories and community structure (Martin, 1988a, b, 1995).

In order to test hypotheses regarding the significance of nest predation to bird populations, the basis for variation in nest predation rates must be discovered. One

influential attempt in this regard is the hypothesis that nest predation increases with proximity to a habitat discontinuity, or an *edge* between two habitats (Gates and Gysel, 1978; Yahner, 1988). The first evidence for this phenomenon was presented in 1978 by J. E. Gates and L. W. Gysel, who found support with observational data from passerines in three study sites in Michigan. The notion of an “edge effect” had been suggested earlier, in relation to species density and diversity rather than nest predation, by Leopold (1933, p. 132). Population densities were subsequently found to increase near habitat edges in birds (Lay, 1938; Good and Dambach, 1943), but also in suspected nest predators (Bider, 1968). Gates and Gysel (1978) provided a plausible argument for a ubiquitous edge effect on nest predation based on this earlier literature and their own results. Together with the concept that nest predation is density dependent (Krebs, 1971; Fretwell, 1972; Göransson et al., 1975; Dunn, 1977), Gates and Gysel (1978) suggested that habitat edges may function as “ecological traps” for nesting birds. Thus, their “ecological trap” hypothesis consisted of three proposed processes, the last of which is resultant from the first two:

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an edge effect on bird nesting density, density dependent nest predation, and an edge effect on nest predation. The present review concentrates on the last of these processes, regardless of the factors responsible for its occurrence. In the 20 years following Gates and Gysel (1978), over 50 empirical tests of an “edge effect on nest predation” have been published.

Many papers claim the existence of a general edge effect on nest predation (e.g. Wilcove et al., 1986; Yahner, 1988; Laurance and Yensen, 1991; Askins, 1994, 1995; Latta et al., 1995; Arcese et al., 1996; King et al., 1996; Niemuth and Boyce, 1997; Suarez et al., 1997; Cooper and Francis, 1998; Huhta et al., 1998; Sloan et al., 1998). The primary object of this paper is to determine the extent to which this “edge effect on nest predation” hypothesis has been substantiated by two decades of research. Three hypotheses will be assessed in a preliminary fashion as to their degree of consistency with available empirical work: (1) nest predation rates increase near habitat edges; (2) the existence of an edge effect varies according to the type of habitat edge; and (3) the existence of an edge effect varies according to the level of habitat fragmentation at the landscape scale.

## 2. Methods

I reviewed 55 widely available, conclusive empirical tests of the “edge effect on nest predation” hypothesis, published between 1978, when the hypothesis was proposed, and 1998. Less than half of these studies have been included in past reviews of the subject (Paton, 1994; Andrén, 1995).

Two issues not considered here are the hypothesized effects on nest predation rates of habitat patch area (e.g. Duebbert and Lokemoen, 1976; Levenson, 1981; Wilcove, 1985) and extent of landscape fragmentation (e.g. Andrén et al., 1985; Yahner and Scott, 1988; Robinson et al., 1995). Although sometimes viewed as indirect assessments of the edge effect, these issues are in fact distinct. Sites have exhibited an area effect without an edge effect (Small and Hunter, 1988; Arango-Vélez and Kattan, 1997) and vice versa (Rudnický and Hunter, 1993). Sites have also exhibited an effect of landscape fragmentation distinct from patch-scale edge and area effects (Kurki and Linden, 1995; Donovan et al., 1997).

Brood parasites such as the brown-headed cowbird *Molothrus ater* are known to affect the reproductive success of some avian species (e.g. Payne and Payne, 1998), and brood parasitism rates may increase near habitat edges (e.g. Brittingham and Temple, 1983; Hahn and Hatfield, 1995). As my focus here is specifically on predation, tests of brood parasitism are not considered. However, brood parasites can also perform nest predation, even on nests they apparently do not parasitize (Scott et al., 1992). It is possible, then, that brood

parasites have been responsible for some of the unidentified predation in the studies under consideration.

Only qualitative assessments of hypotheses can properly be offered here. Comparisons of numbers or percentages of sites, including Chi-square ( $\chi^2$ ) one-sample tests, are intended as indications of empirical results, and not as rigorous statistical tests of hypotheses. The reason for this is that studies reviewed here vary widely in several aspects of methodology (e.g. experiment vs. observation, size and number of eggs, exposure period, nest density, construction and location of nests, length and sample size of transects, patch and site characteristics). Recently, attempts have been made to gain an understanding of how nest and habitat variables contribute to an edge effect on nest predation by statistical meta-analysis (Hartley and Hunter, 1998; Söderström et al., 1998). Such results, though suggestive, are necessarily compromised to the extent that the studies reviewed fail to meet the central assumption of meta-analysis, which is similarity of methodology. The value of statistical meta-analysis in this area will increase only if the many ways in which the studies differ in methods, data, and site can be quantified and controlled, if the direction of any effect (even if nonsignificant) always appears in the results, and if enough additional studies are performed to increase the sample size relative to each variable. Therefore, this review does not involve reanalysis or pooling of results. Rather, the authors' own statistical analysis was used, with the exception of Best (1978) and Wilcove et al. (1986), which were analyzed in Paton (1994). Results of studies reviewed are based on a level of significance of  $P < 0.05$  unless otherwise indicated. Two advantages of this approach are that results from all available studies can be surveyed, and that no inappropriate assumptions for reanalysis or meta-analysis are made. The major disadvantage of this approach is that only qualitative and preliminary conclusions can be drawn.

Another disadvantage of reviewing many studies in an area where no consensus has been reached as to protocol, is that methodological differences may underlie apparent inconsistencies among studies. In nest predation studies the possibility of differences between nest predation rates on artificial and natural nests (e.g. Lenington, 1979; Reitsma et al., 1990; Sloan et al., 1998), and the possibility of artifactual influences of the types of eggs used (e.g., Roper, 1992; Haskell, 1995; Major and Kendal, 1996) have been sources of concern. A comparison among the studies reviewed here reveals no consistent differences in the likelihood of an edge effect for either of these methodological factors, as Andrén (1995) concluded for artificial versus natural nests. However, the possibility remains that nest type and location, as well as egg type, could result in predation by different species, which could then translate into differences in the likelihood of an edge effect.

### 3. Results and discussion

#### 3.1. General status of edge effect hypothesis

The edge effect on nest predation hypothesis would predict a preponderance of studies to conclude that rates of nest predation increase with proximity to habitat edges. Of 55 studies, 13 (24%) found a significant edge effect in any test conducted, 32 (58%) did not find a significant edge effect, and 10 (18%) were multifactorial studies in which results were mixed, such that an edge effect was demonstrated in at least one treatment but was not in at least one other (Table 1). Four studies were conducted on the same or nearby sites (Yahner and Wright, 1985; Yahner, 1991; Yahner et al., 1993; Yahner and Mahan, 1997), whereas one study tested three distant study sites (Berg et al., 1992). Focusing on sites rather than studies, in order to insure statistical independence among studies, yields the same result. Of 54 study sites at least 8 km apart (and over 30 km apart with two exceptions: see Table 1, footnote d), 13 (24%) exhibited a significant edge effect in any test conducted, 31 (57%) did not exhibit a significant edge effect, and 10 (19%) were subject to multifactorial studies in which results were mixed, such that an edge effect was detected in at least one test but was not in at least one other. Of the sites which did not support the edge effect on nest predation hypothesis, five exhibited a significant *decrease* in predation with proximity to the edge, in at least one treatment (Table 1, footnote c). Therefore, the majority of empirical tests have not supported the edge effect on nest predation hypothesis. The number of study sites which do exhibit a strong edge effect suggest, however, that in some situations a phenomenon is occurring that is related either directly or indirectly to the existence of a habitat edge.

#### 3.2. Edge type

Some have suggested that the diversity of types of habitat edges may at least partially underlie the disparity among empirical tests of the edge effect on nest predation hypothesis (Angelstam, 1986; Andrén, 1995; Murcia, 1995). Perhaps some kinds of habitat discontinuity generally exhibit an edge effect whereas others do not. If this is true, then a categorization of studies according to edge type, in terms of the nature of the two adjoining areas, should reveal this phenomenon (Table 1). In 23 different edge types which are combinations of seven different types of habitat with 11 classes of adjacent terrain, there is no edge type for which an edge effect has been demonstrated consistently across study sites. In fact, aside from one edge type (grassland-fenceline) for which only one study was performed, there is not one edge type for which the edge effect on nest predation hypothesis is more often supported than

rejected. On the other hand, the edge effect has been more often rejected than supported in five edge types for which only one study was performed, and 12 edge types which have received multiple tests. In the most heavily researched edge type, forest/agricultural edges, for which a general edge effect has been concluded in past reviews (Wilcove et al., 1986; Paton, 1994; Andrén, 1995), the 14 available studies (corresponding to 14 independent sites) are in fact divided evenly in their results. The discrepancy between this and earlier reviews is to some extent due to the predominantly negative results of the most recent studies (in 1997–1998, 13 studies were published which tested 25 edges, and only seven of these produced evidence for the edge effect on nest predation). Although forest/agricultural edges are just as likely as not to exhibit an edge effect, a likelihood of 50% is much higher than that of habitat edges in general, and explains the particularly high level of concern which has surrounded that type of edge with regard to this hypothesis. Still, the general hypothesis that certain edge types, in terms of the nature of the adjoining habitats, are consistently prone to an edge effect while others are not, is not substantiated by the literature.

Angelstam (1986) suggested that an edge effect on nest predation is most likely to occur where there is a steep gradient in primary productivity across the edge (e.g. forest/agriculture and forest/grassland edges) and is least likely to occur where this gradient is less pronounced (e.g. agriculture/grassland edges). Productivity in this case indicates vegetational structure or type; a nest predator may be more likely to respond to a habitat discontinuity when the change in the plant community across the edge is more pronounced. A preliminary test of this hypothesis can be conducted by comparing the empirical results at those edge types involving a steep primary productivity gradient (the majority of the literature) with those edge types involving a relatively slight gradient. Edge types associated with the miscellaneous categories of “wetlands” and “various open areas”, which may represent a wide variation in primary productivity, and field/fenceline edges where the adjacent terrain is very narrow, will be excluded here (except for Small and Hunter, 1988, where land edges and wetland edges were analyzed separately). Forests, in general, are much higher in primary productivity (generally by at least 500 g/m<sup>2</sup>/year) than agriculture, oldfield, or grassland of the same latitude (Whittaker and Likens, 1973). A provisional test of Angelstam’s hypothesis involves separating edge types comprised of forest adjacent to such open land, from edge types comprised of two types of adjacent forest or two types of adjacent open habitat. When this is done, 43 tests of edges with steep primary productivity gradients are distinguished from seven tests of low primary productivity gradients (including nine sites where more than one edge type was tested and analyzed separately). Among tests of high-gradient

Table 1  
Correlation of nest predation rate with proximity to habitat edge, categorized by edge type

Habitat	Adjacent terrain	Increase in nest predation near edges	No increase in nest predation near edges
Forest	Agriculture	Gates and Gysel, (1978) Wilcove et al., (1986) (analyzed in Paton, 1994) Andrén and Angelstam, (1988) Temple and Cary, (1988) Møller, (1989) <sup>a</sup> Björklund, (1990) Sandström, (1991) <sup>d</sup> Donovan et al., (1997) <sup>b,f</sup>	Angelstam, (1986) Møller, (1989) <sup>a</sup> Santos and Tellería, (1992) Nour et al., (1993) Arango-Vélez and Kattan, (1997) <sup>b,c</sup> Bayne and Hobson, (1997) <sup>b</sup> Danielson et al., (1997) <sup>e</sup> Donovan et al., (1997) <sup>b,f</sup>
Forest	Grassland	Linder and Bollinger, (1995) Donovan et al., (1997) <sup>b,f</sup>	Gibbs, (1991) Laurance et al., (1993) Donovan et al., (1997) <sup>b,f</sup>
Forest	Wetland	Fenske-Crawford and Niemi, (1997) <sup>b,d</sup>	Small and Hunter, (1988) Vander Haegen and DeGraaf, (1996) Pöysä et al., (1997) Huhta et al., (1998) <sup>b</sup>
Forest	Clearcut	Rudnický and Hunter, (1993) <sup>g</sup> King et al., (1996) <sup>h</sup> Fenske-Crawford and Niemi, (1997) <sup>b,d</sup> Yahner and Mahan, (1997) <sup>d</sup>	Ratti and Reese, (1988) Storch, (1991) <sup>c</sup> Rudnický and Hunter, (1993) <sup>g</sup> Bayne and Hobson, (1997) <sup>b</sup> Huhta et al., (1998) <sup>b</sup>
Forest	Young/regenerating forest	Gibbs, (1991)	Yahner and Wright, (1985) <sup>d,i</sup> Yahner, (1991) <sup>d,i</sup> Laurance et al., (1993) Yahner et al., (1993) <sup>d,i</sup> Hanski et al., (1996) <sup>d</sup>
Forest	Suburban development		Arango-Vélez and Kattan, (1997) <sup>b,c</sup> Danielson et al., (1997) <sup>e</sup>
Forest	Powerline clearing	Chasko and Gates, (1982) <sup>e,j</sup>	Chasko and Gates, (1982) <sup>e,j</sup>
Forest	Road	Burkey, (1993)	Huhta, (1995) Latta et al., (1995) Yahner and Mahan, (1997) <sup>e,d</sup>
Forest	Various open areas	Hannon and Cotterill, (1998) <sup>k</sup>	Kuitunen and Helle, (1988) Small and Hunter, (1988) <sup>c</sup> Hanski et al., (1996) <sup>d</sup> Hannon and Cotterill, (1998) <sup>k</sup> Wong et al., (1998)
Agriculture	Forest	Møller, (1989)	Andrén and Angelstam, (1988) Berg, (1992) Vickery et al., (1992)
Agriculture	Grassland		Mankin and Warner, (1992) <sup>b</sup>
Grassland	Forest	Burger et al., (1994)	Best, (1978) (Fig. 4, analyzed in Paton, 1994) Mankin and Warner, (1992) Söderström et al., (1998) <sup>d</sup>
Grassland	Agriculture		Mankin and Warner, (1992) <sup>b</sup> Pasitschniak-Arts et al., (1998) <sup>b</sup> Pasitschniak-Arts et al., (1998) <sup>b</sup>
Grassland	Wetland	Crabtree et al., (1989)	
Grassland	Fenceline	Yosef, (1994)	
Grassland	Road		Mankin and Warner, (1992) Pasitschniak-Arts et al., (1998) <sup>b</sup>
Grassland	Various open areas	Pasitschniak-Arts and Messier, (1995) <sup>l</sup> Pasitschniak-Arts and Messier, (1996) <sup>m</sup>	Pasitschniak-Arts and Messier, (1995) <sup>l</sup> Pasitschniak-Arts and Messier, (1996) <sup>m</sup>
Shrub, moor	Forest	Niemuth and Boyce, (1997)	Avery et al., (1989) <sup>n</sup>
Shrub, moor	Various open areas		Rogers, (1994)
Wetland	Forest		Berg et al., (1992) <sup>o</sup> Esler and Grand, (1993)
Wetland	Open upland		Picman et al., (1993)
Clearcut	Forest		Ratti and Reese, (1988)
Powerlines	Forest		Chasko and Gates, (1982) <sup>e,c</sup>

(continued on next page)

Table 1 (continued)

- <sup>a</sup> Positive result with uncovered nests, negative result with partially covered nests.
- <sup>b</sup> A single test is represented under two or more edge types because the authors pooled data for different edge types (see other listing of the same reference and footnote); all other multiple listings of references refer to separately analyzed tests.
- <sup>c</sup> At least one treatment resulted in a significant inverse edge effect; predation was higher in the habitat interior than on the edge.
- <sup>d</sup> The four studies of Yahner and associates were performed in the same area and so are not statistically independent. Sites used by Hanski et al. (1996) and Fenske-Crawford and Niemi (1997) were approximately 8 km apart. Sites used by Sandström (1991) and Söderström et al. (1998) were approximately 20 km apart. All other studies utilized sites > 30 km apart from each other.
- <sup>e</sup> Tested at the  $P < 0.1$  level of significance (all others  $P < 0.05$ ).
- <sup>f</sup> Positive result in moderately fragmented landscapes (45–55% forest cover), negative result in landscapes with high (< 15% forest cover) or low (> 90% forest cover) fragmentation.
- <sup>g</sup> Positive result with shrub nests, negative result with ground nests.
- <sup>h</sup> Reflects a trend at  $P = 0.1$ .
- <sup>i</sup> Results reflect stands of varying ages both in the nesting habitat and in the adjacent area.
- <sup>j</sup> Positive result in one study site and negative in another similar to it but with subtle differences in prey distribution and corridor vegetation characteristics.
- <sup>k</sup> Negative result with all nests or with nests depredated by mammals only; positive result with nests depredated by corvids only.
- <sup>l</sup> Positive result in fields with dense nesting cover, negative result in idle pasture or delayed hayfields.
- <sup>m</sup> Positive result in large (200 ha) plots, negative result in small (50 ha) plots.
- <sup>n</sup> Initial positive result was completely explained by a vegetational variable.
- <sup>o</sup> Three distant (> 250 km) and so statistically independent study areas were used. One out of six plots exhibited an edge effect, but another exhibited an inverse effect; all others exhibited no effect.

edges, 18 (42%) found an edge effect in at least one treatment, and 25 (58%) did not. Most sites adjacent to terrain with very different primary productivity have not exhibited an edge effect. Among the few (7) low-gradient edge sites, only one of these studies found an edge effect. That study (Gibbs, 1991) was performed in a highly productive tropical rainforest. Although Gibbs (1991) provided no information regarding the age of the secondary growth, the gradient between primary and secondary growth might be as great or greater than that between a temperate forest and field. If this is so, then no study with a low (< 500 g/m<sup>2</sup>/year) primary productivity gradient across the edge has exhibited an edge effect on nest predation. The first prediction of Angelstam's hypothesis is that an edge effect will occur where there is a steep gradient of primary productivity across the edge. This is not supported by empirical studies. The second prediction of his hypothesis is that an edge effect will not occur where there is a shallow gradient. This is consistent with empirical work, but only seven such tests have been published to date. Moreover, separating the sites by the magnitude of their vegetational gradient does not significantly change the proportion of studies exhibiting an edge effect from that of all sites taken together ( $\chi^2 = 0.54$ , d.f. = 1,  $P > 0.2$ ).

One more hypothesis regarding edge types and their relationship with the edge effect on nest predation hypothesis is that forest/agriculture and forest/grassland edges are more likely to exhibit an edge effect than forest/clearcut edges, for two proposed reasons. The first is that forest/clearcut edges do not possess a gradual or "feathered edge" (Ratti and Reese, 1988) which can support edge-loving, or ecotonal, predators (Rudnicki and Hunter, 1993). The second proposed reason is that clearcuts resemble natural light gap disturbances and are too temporary to maintain a community of pre-

dators distinct from that of the intact forest (Bayne and Hobson, 1997). Table 1 demonstrates that the proportion of positive to negative results with respect to the edge effect on nest predation is 9–10 at forest/agriculture or forest/grassland edges, and is 4–5 at forest/clearcut edges (all studies in each category representing independent sites). Therefore, the hypothesis that forest/agriculture and forest/grassland edges are more likely than clearcut edges to exhibit an edge effect is not supported by empirical work.

### 3.3. Extent of landscape fragmentation

Nest predation rate may depend on the degree of fragmentation of the landscape, as distinct from smaller scale edge and patch area data (Kurki and Linden, 1995; Hartley and Hunter, 1998). Donovan et al. (1997) found an edge effect on nest predation in landscapes where 45–55% of the area was suitable prey habitat, but not in landscapes where < 15 or > 90% of the area was suitable prey habitat. In this case forest-nesting migratory songbirds were the focal prey species, so forest cover was considered suitable prey habitat. The authors introduced the hypothesis that "percentage of forest cover at the landscape scale influences predation levels and the existence of edge effects" (ibid., p. 2070). If the latter half of this hypothesis is true, variability in the existence of an edge effect should be explained by a division of study sites according to the percentage of suitable prey habitat that is present on the landscape scale.

What is considered "suitable prey habitat" varies from study to study, and for purposes of this review it is simply considered the habitat type in each study where nests were sought (or placed, in artificial nest studies). In some artificial nest studies a focal habitat could not be determined, as when nests were placed on both sides

Table 2  
Tests of the edge effect on nest predation hypothesis by extent of habitat fragmentation<sup>a</sup>

Fragmentation extent	# (%) positive	# (%) mixed	# (%) negative
High (11 sites)	4 (36)	3 (27)	4 (36)
Moderate (22 sites)	4 (18)	3 (14)	15 (68)
Low (10 sites)	1 (10)	2 (20)	7 (70)
All studies (54 sites)	12 (22)	11 (20)	31 (57)

<sup>a</sup> “High” indicates <50% focal prey habitat on the landscape level (as defined by the study) and “low” indicates >75% habitat. “Moderate” refers to sites with an intermediate (50–75%) amount of habitat on the landscape. All study sites are considered part of single landscapes, so some large study sites which are listed here as “moderate” might consist of portions of differing fragmentation extents. “Positive” studies have concluded an edge effect in all tests performed, “mixed” have concluded an edge effect in at least one treatment but not in at least one other, and “negative” have not found any edge effect.

of an edge and no mention was made of model bird species; these studies were excluded from this part of the analysis. Likewise, the studies themselves were the basis for determining the extent and nature of the “landscape”. Only studies which provided either quantitative data for percentage of prey habitat on the landscape, or qualitative descriptions or maps from which an estimate could be drawn, were included in the analysis. Landscapes with less than 50% prey habitat (i.e. landscapes dominated by a matrix that is presumed to be hostile relative to the prey habitat type) are considered highly fragmented. Landscapes with over 75% prey habitat are considered areas of low fragmentation. This division allows the sites with high and low fragmentation to comprise two groups of approximately equal size. Landscapes which fall between these extremes, containing 50–75% habitat, are considered moderately fragmented. Because of the imprecision of those estimates from qualitative descriptions and maps, as well as the fact that many studies were performed in several sites of varying fragmentation, the present hypothesis (that differences in extent of landscape fragmentation underlie the variability in the existence of an edge effect on nest predation) can be tested only in a preliminary way until more studies are performed that explicitly vary the amount of fragmentation at the landscape level.

Seven of 11 (63%) sites exhibited an edge effect in at least one test treatment in highly fragmented landscapes, as compared with only three of 10 (30%) in landscapes of low fragmentation (Table 2). Landscapes of moderate fragmentation have intermediate proportions of sites exhibiting an edge effect on nest predation. These findings are suggestive, although the differences in the number of sites exhibiting an edge effect in landscapes of different levels of fragmentation are not statistically significant ( $\chi^2=1.6$ , d.f.=2,  $P>0.1$ ). A correlation of fragmentation with the edge effect on nest predation might be expected, for example, if nest predators are

infiltrating the avian habitat from the outside, for their populations would then respond positively to the amount of matrix (nest predator habitat) on the landscape (Andrén, 1992).

Donovan et al. (1997) applied their predictions regarding the effect of habitat fragmentation on nest predation to forest habitats alone. If nonforest habitats are excluded, the pattern demonstrated by Table 2 is amplified. The only sites to exhibit an edge effect in a forest on a landscape of low fragmentation (of 6) have been 1 with mixed results and 1 at  $P=0.1$ . On the other hand, in highly fragmented forests, all five sites exhibited an edge effect in at least one treatment. The sample size is inadequate for statistical comparison. Too few studies have been performed in agriculture, oldfield, prairie, shrub, and wetland habitats to analyze these habitats separately.

#### 4. Conclusions

Although many studies have found higher nest predation near habitat edges, the majority of studies have not. Two further hypotheses have often been tested in nest predation studies: that the type of edge (in terms of the nature of the adjoining plant communities) and the extent of fragmentation of the landscape, respectively, can account for the variation in the existence of an edge effect. Empirical evidence has not clearly supported either hypothesis, but there is a trend towards a positive correlation of the existence of an edge effect with degree of landscape fragmentation, especially in forested landscapes. With regard to the relationship between edge type and the existence of an edge effect, the only statement that can be justified to any extent by studies to date, and this only on the basis of seven studies, is that an edge effect is very rare, perhaps nonexistent, where the adjoining plant communities have a low gradient in primary productivity. No edge effect has been found in sites where forests of different ages were the adjoining habitats, except for one tropical site where the gradient is unknown. Likewise the two studies which test agriculture–grassland edges and their edges with roads have not found an effect (Table 1). This may be due to the fact that nest predators range indiscriminately across borders between habitats which are similar in physiognomy, not recognizing them as habitat discontinuities. This idea of a lack of predator recognition of certain edges may be tested by tracking predators, as well as by nest predation studies which compare rates across habitat types that are structurally similar.

These results suggest that our knowledge about the efficacy of the edge effect on nest predation hypothesis has grown since the publication of two prior reviews [Paton, 1994 (21 studies); Andrén, 1995 (27 studies)]. Paton (1994) concluded, in agreement with Wilcove et

al. (1986), that the generalization that nest predation increases near habitat edges was warranted. The lack of evidence provided by four artificial nest studies was explained with reference to inadequate experimental design. In contrast, the present review suggests that although an edge effect on nest predation occurs in some sites, it is not a valid generalization, regardless of the habitat under consideration. Problems in experimental design are indeed present in nest predation studies, and could be contributing to the lack of consensus (Murcia, 1995). However, the fact that 42 of 55 studies (76%) found no evidence for an edge effect in at least one treatment suggests that design problems alone are not responsible for the failure of studies to detect an edge effect. Comparison with Andrén (1995) is more difficult because that study analyzed edge effects and patch size effects together. Andrén (1995) found that edge-related increase in nest predation primarily occurred near forest/agriculture edges, and generally not in forest mosaics. Therefore Andrén (1995) claimed that the literature lends some support to Angelstam's (1986) hypothesis that edge effects occur where a steep gradient in productivity exists across the edge. The present review provides some support for the gradient hypothesis as well, but research since Andrén (1995) has shed doubt on the claim that forest/agriculture edges are consistently prone to edge effects. According to the studies reviewed here, such edges may be just as likely not to exhibit an edge effect on nest predation as to exhibit one. Nevertheless, Andrén (1995) realized that many sites are not likely to exhibit an edge effect, and introduced explanations as to why edge effects may be found in some areas and not others, based on habitat and predator considerations. The results of the present review highlight the need for such reasoning and the testing of such hypotheses.

Two notes of caution should be noted regarding the results presented here. First, studies of the edge effect on nest predation range widely in their plot sizes, and in many cases the sizes of plots were mixed or not provided in the publications. As one study found plot size to be a significant influence on the existence of an edge effect on nest predation (Pasitschniak-Arts and Messier, 1996), the variation in plot size among studies could complicate comparisons. Second, and similarly, studies differ widely in the distance from the edge into the habitat that nest predation was tested. Most (38) studies went at least 100 m into the habitat, to a maximum of 1500 m; the remainder went less than 100 m (nine studies) or provided insufficient information in this regard (eight studies). Researchers have proposed a variety of distances to which an edge effect might extend into a habitat patch (e.g. >200 m in Wilcove et al., 1986, vs. ~50 m in Paton, 1994).

Although the statement is tautological that nest predation dynamics depend on the activity of the predators

involved, only recently have serious attempts been made in nest predation studies to assess the nature of the nest predator guild in each study site. Little can be concluded yet regarding species-specific predator differences, however, for only 22 of 55 studies of the edge effect have provided information on nest predator assemblage with some degree of reliability, and only 13 of these identified predators beyond class level. Claims are often made, for instance that avian nest predators generally have an affinity to edges whereas mammalian predators do not (Nour et al., 1993; Marini et al., 1995). Determining whether this hypothesis describes a general ecological phenomenon depends on continued study including reliable predator identification. A model study in this respect is Hannon and Cotterill (1998), who were able to separate instances of bird and mammal predation and analyze the dynamics of each class of predator separately. A few other studies have focused on species-specific nest predator differences and by so doing have been able to provide explanations for often complex results. These studies include Angelstam (1986) and Møller (1989), who found striking differences in edge-affinity among corvid nest predators. Several other studies have been performed in primarily mammal-dominated sites (Laurance et al., 1993; Picman et al., 1993; Pasitschniak-Arts and Messier, 1995, 1996; Hanski et al., 1996; Vander Haegen and DeGraaf, 1996; Bayne and Hobson, 1997; Fenske-Crawford and Niemi, 1997; Hannon and Cotterill, 1998). In some cases even within a given predator species the response to edges varies according to landscape features, such as the proximity to suburban areas (Danielson et al., 1997) or the amount of core habitat (i.e. habitat far from edges) available (Donovan et al., 1997).

Regardless of whether there are particular landscape conditions or predator assemblages that favor an increase in predation on avian nests near habitat edges, the hypothesis that an edge effect on nest predation is a universal ecological phenomenon is not supported by available experimental and observational data. Contrary to generalizations that are widespread in the literature (e.g. Wilcove et al., 1986; Yahner, 1988; Laurance and Yensen, 1991; Askins, 1994, 1995; Latta et al., 1995; Arcese et al., 1996; King et al., 1996; Niemuth and Boyce, 1997; Suarez et al., 1997; Cooper and Francis, 1998; Huhta et al., 1998; Sloan et al., 1998), the majority of study sites exhibit no increase in nest predation rate near edges; in a few sites, nest predation actually decreases near edges. Chasko and Gates (1982, p. 6) stated that "In the past, it has been assumed that edge habitat had high suitability for certain avian species". They then suggested that this older perspective be reevaluated because of the newly recognized danger of edge-related nest predation, as evidenced by Gates and Gysel (1978). However, in the two decades following the initial test of the edge effect on nest predation, the atti-

tudes of many towards edge habitat swung too far in the opposite direction despite the empirical evidence. Many have been incorrectly assuming that edge habitat always has very low suitability for avian species, a claim which is as unsubstantiated by the results of empirical tests as its inverse. In retrospect on those 20 years of testing, little predictive ability with regard to nest predation dynamics is forthcoming from a scrutiny of habitat edges per se. Researchers may gain greater insight in the future, as a few have already, by first determining which predators are most active in their study sites, and then focusing on their behavior and its relation to habitat and landscape features, including habitat edges.

Studies could be designed with an aim of developing a body of knowledge of species-specific patterns of nest predation. The limited success of tests for general effects of habitat edge without knowledge of the dominant nest predators in the study area, suggests that initially identifying and determining the relative importance of nest predators may be a more successful approach. Using what is known of the behavior of these species, predictions can be made regarding patterns of nest predation in a study area, including response to habitat edges (as well as other effects, such as nest density, patch size, and nest height). If little is known of the the predation patterns of a given nest predator, experiments could be designed which bias nest predation in favor of certain species. Ideal study sites for this objective are where a single predator is known to be almost exclusively responsible for nest predation. Ultimately, when the dominant predators have been identified and their typical patterns of predation are known, land areas can be categorized into nest predation types. This categorization will be complex in cases where more than one nest predator is important, or when the predation patterns of a single species depend on landscape or habitat factors. In this way, researchers can generalize across similar study areas and make specific and testable predictions as to patterns of nest predation. Conclusions would be valuable when considering bird species most at risk of nest predation in an area, and the probable effect of an increase or decrease in a given nest predator population (e.g. as a result of development or a change in management practices) on the breeding bird community.

With regard to study areas, very few studies have been performed in nonforest habitats, or in habitats south of 40°N. In artificial nest studies, care should be taken to place nests within 10 m of an edge, and place the furthest nests beyond 50 m from the edge, if an objective is to test for the existence of an edge effect. The nest, eggs, and nest site should be designed to mimic a model species in the study area. Explicit information should be provided in publications as to the nature of the adjoining habitats, the extent of fragmentation of the landscape, habitat patch sizes, predator identification, and statistical significance.

Managers interested in assessing and responding to nest predation risk will benefit from classifying their reserves according to dominant nest predators. They should be aware of those species' typical patterns of nest predation, and the implications for habitat edges and other factors. On the basis of this information an inference can be drawn as to what bird species are most at risk. If birds are an important target of conservation, the size, shape, and management plans of reserves should depend not only on the habitat requirements of those birds, but also on the patterns of nest predation in the area. For example, if nest boxes are a significant part of a management plan, knowing the pattern of nest predation in an area can help to determine safer locations for the boxes. Perhaps most importantly, edges are not necessarily detrimental to the reproduction of birds, even of forest birds nesting near a border of an agricultural field. Heterogeneous habitats should therefore be considered as potentially important and successful breeding areas for some birds. Future research is necessary in order for managers to be able to predict reliably the effect habitat edges have on breeding birds in any given area.

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