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HABITAT EDGES AND AVIAN ECOLOGY: GEOGRAPHIC PATTERNS AND INSIGHTS FOR WESTERN LANDSCAPES

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Abstract. Habitat edges are an important feature in most terrestrial landscapes, due to increasing rates of habitat loss and fragmentation. A host of hypothesized influences of habitat edges on the distribution, abundance, and productivity of landbirds has been suggested over the past 60 years. Nevertheless, "edge effects" remains an ill-defined concept that encompasses a plethora of factors thought to influence avian ecology in heterogeneous landscapes. The vast majority of research on edge effects has been conducted in the broad-leafed forests of northeastern and midwestern North America. In general, many western habitats are more heterogeneous and naturally fragmented than their eastern counterparts, and habitat edges are a ubiquitous component of most western landscapes. These differences in landscape structure suggest that edge effects, and the mechanisms underlying them, may differ markedly in the West. We examined over 200 papers from the peer-reviewed literature on edge effects, focusing our efforts on empirical results and trends in research approaches. The relative dearth of western studies makes geographic comparisons difficult, but it is clear that mechanistic understanding of edge effects has lagged behind pattern identification. Bird responses to edge effects tend to vary markedly among species and among different edge types, while no clear pattern emerges regarding species diversity. In the context of the review, we discuss research and modeling approaches that could move our understanding of edge effects toward a more mechanistic and predictive framework.

Key Words: core area model; density; edge effects; effective area model; habitat edge; habitat fragmentation; heterogeneity; species diversity.

Habitat fragmentation increases landscape heterogeneity as continuous patches of native habitats are broken into numerous smaller, isolated patches surrounded by a matrix of different, often heavily disturbed or anthropogenic habitats (Wilcox 1980, Wilcove et al. 1986, Wiens 1994, Franklin et al. *this volume*). The loss of native habitat cover and the increasing isolation of the resulting patches from one another have been the subject of numerous empirical and theoretical studies and several reviews (e.g., Saunders et al. 1991, Faaborg et al. 1995). Since the early 1970s these two factors have dominated debates about conservation planning in increasingly fragmented landscapes (e.g., Diamond 1976; Simberloff and Abele 1976, 1982; Terborgh 1976).

Another result of habitat fragmentation is an increase in the amount of edge habitat, as well as the proliferation of new types of edges, as anthropogenic habitats (e.g., agriculture, logged forest, and urbanized areas) replace native habitats and abut the remaining fragments. The increasing number of smaller patches, and the linear or irregularly shaped patches that often result from fragmentation (Feinsinger 1997), contribute to the rapid, often exponential increase in the amount of edge habitat in the landscape (Fig. 1).

Implications of the proliferation of edge habitat for bird populations are numerous, ranging from the alteration of microclimatic conditions to changes in interspecific interactions, such as competition, predation, and nest parasitism. These and other edge effects are often distinct from the effects associated strictly with the loss of habitat and the increasing isolation of the remaining patches. By influencing the quality of nearby habitat in the remaining fragments, edges may also directly affect the amount of available suitable habitat (Temple 1986, Sisk et al. 1997). Thus, edge effects constitute a class of impacts that are of increasing importance as fragmentation advances and the heterogeneity and structural complexity of the landscape increases.

Despite over 60 years of active research, our understanding of edge effects remains diffuse and largely site-specific. Interestingly, the literature on "edge effects" predates research on habitat fragmentation by some 45 years, and because of this long history, a summary of the literature on edge effects parallels the development of avian ecology in general. In fact, edge effects can be viewed as the earliest attempt to study avian ecology at the landscape scale, a perspective that received less attention as the focus of field ecology shifted to population dynamics and community ecology in the 1950s through the 1970s. The conservation imperative that emerged in the seventies, driven by the recognition of rapid habitat loss and fragmentation, returned consideration of edge effects to the forefront of avian research, but in a very different context.

Our overview of edge effects traces the development of conceptual approaches through field studies, experiments, and modeling ap-

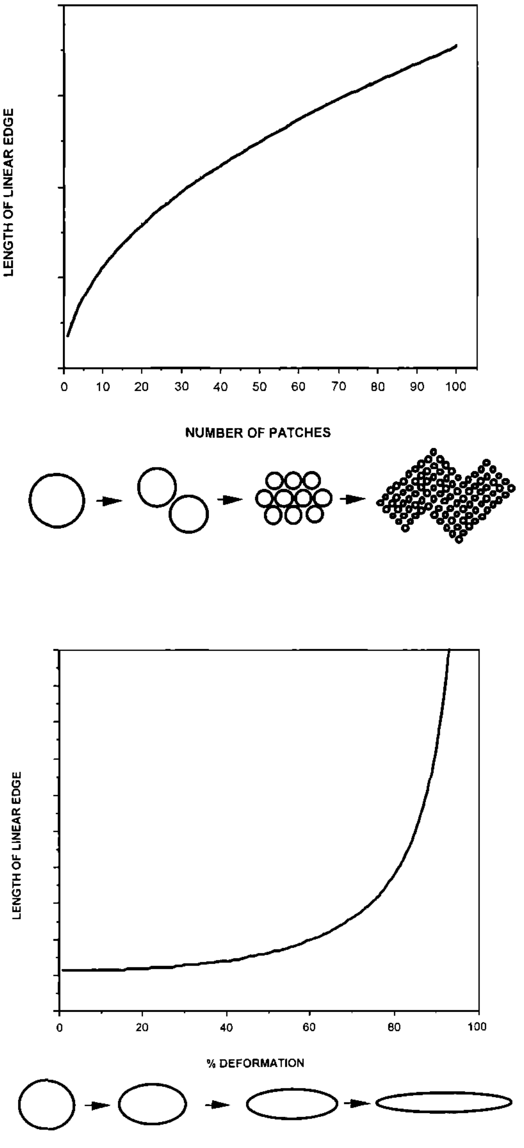


FIGURE 1. Edge habitat proliferates with increasing fragmentation, due both to the increased edge per unit area as the number of patches increases (top), and as individual patches become, on average, more linear or irregularly shaped, as represented here as an increasingly flattened patch (bottom). From Sisk and Margules (1993).

proaches. The paper focuses on patterns in the literature, particularly the disparity in the level of research in the eastern and western United States and the emphasis upon certain habitat types. We list working hypotheses derived from the literature, and we provide brief summaries of supporting and refuting evidence. Finally, we examine more predictive approaches to the study of edge effects so that the accumulated knowledge might be put to work in efforts to predict the impacts of ongoing fragmentation. Our ultimate goal is to incorporate a consideration of edge effects into efforts to reverse the negative impacts of fragmentation and improve reserve designs, restoration efforts, and management plans for the conservation of avian biodiversity.

EDGE EFFECTS—AN ILL-DEFINED "LAW" OF ECOLOGY

"Edge effect" is among the oldest surviving concepts (some would say "buzz-words") in avian ecology. In 1933, Leopold referred to "the edge effect" to explain why quail, grouse, and other game species were more abundant in patchy agricultural landscapes than in larger fields and forested areas (Fig. 2). He hypothesized that the "desirability of simultaneous access to more than one (habitat)" and "the greater richness of (edge) vegetation" supported higher abundances of many species and higher species richness in general (Leopold 1933). This common-sense definition drew on years of experience as a forester and game manager, and reflects the focus of early wildlife managers on game species, many of which utilize early successional and/or edge habitats preferentially. Lay (1938) provided some of the earliest empirical evidence supporting both increased abundance and greater species richness at woodland edges. His interpretation of these patterns also began a long tradition of deriving management guidelines from studies of bird abundances and species diversity at edges. His claim that the "maximum development of an area for wildlife requires . . . small but numerous clearings" was accepted by many wildlife managers and found its way into many textbooks over a period of several decades, culminating in what has been called the "law of edge effect" (Odum 1958, Harris 1988). General acceptance of the hypothesis that diversity and abundance are higher near edges led wildlife biologists to advocate the creation of edge under the assumption that it would benefit biodiversity (e.g., Giles 1978, Yoakum 1980, Dasmann 1981). This understanding of the beneficial nature of edge effects influenced land management practices for decades and served as a *de facto* prescription for habitat fragmentation in the name of wildlife management. Even today, land managers frequently advocate the creation of edges via (for example) forest clearing and prescribed fire, with the intention of increasing avian abundance and diversity.

More recently, the relationship between forest fragmentation and both nest predation and parasitism has spawned a different view of edge effects. Edges have been shown to support high-

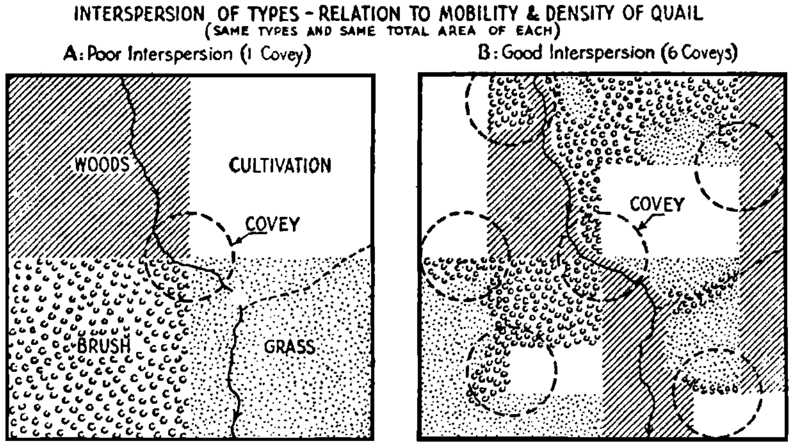


FIGURE 2. Leopold (1933) coined the term "edge effect" to explain increased abundance of game birds in heterogeneous landscapes with many edges. In this figure, 160 ac (64.7 ha) blocks of 4 habitat types, each 40 ac (16.2 ha), are displayed in the two panels. Panel (a) has 2 mi (3.2 km) of edge, while panel (b) has 10 mi (16 km). Leopold argued that greater bird abundances are associated with the heterogeneous landscapes, such as (b).

er rates of nest predation and parasitism (Wilcove 1985, Paton 1994, Andrén 1995). Current texts are likely to present evidence that edge effects are "bad" and that the creation of edge habitat by fragmentation leads to the decline of "interior species" that are particularly susceptible to nest parasites and predators (e.g., Meffe and Carroll 1997). Again, the focus on certain aspects of edge effects (in this case nest predation and parasitism rates) has led to a widely accepted, general rule of edge effects. However, in this case, the supposedly beneficial effects are often ignored, while the adverse effects, demonstrated for a subset of species in particular habitats and in certain geographic areas, are highlighted.

Thus, perceptions of the relationship between edge effects and habitat fragmentation are often contradictory, and the reality is almost always more complex than perceptions. In some cases, edges are thought to benefit birds; in others they are seen as the primary threat to bird diversity. And in cases where edges support high bird density but low nest productivity, edge effects on population persistence may be particularly negative (Ratti and Reese 1988). Nevertheless, the term continues to be applied with little discrimination, and the assumption that all influences of habitat edges can and should be grouped into a uniform class of ecological impacts persists in the literature. The complexity and diversity of the responses of different species to differing edge types, combined with the lack of an inclusive theoretical framework for organizing the plethora of field observations reported in the literature, has turned "edge effects" into a grab-bag term, one that too often is used casually to explain anomalous or inconclusive results. Indeed, the term edge effect has become so widely accepted in the management literature that it is commonly used to explain diametrically opposed observations.

Part of the confusion may result from changes in the scale at which species diversity is assessed. Historically, biologists and planners have focused on alpha (local) diversity, which is often high near habitat edges. As conservation planning has shifted to larger areas, and scientists have assessed regional and global patterns in biodiversity, the focus on species diversity has shifted to the gamma (regional) level, which may be lower in fragmented landscapes due to the loss of edge-avoiding species. Until scientists and managers are able to adopt a multi-scaled approach to assessing biodiversity (see Noss 1990), confusion over edge effects is likely to persist.

HISTORICAL PERSPECTIVES: RESPONSE VARIABLES, FOCAL SPECIES, AND GEOGRAPHIC PATTERNS

METHODS

We reviewed the literature on edge effects dating back to the mid-1930s in an attempt to synthesize the large and diverse body of published work in avian ecology and wildlife management. Drawing from online searches, published abstracts, examination of literature cited in all papers reviewed, and inquiries with colleagues, we created an annotated bibliography to facilitate analysis of patterns from published studies of edge effects. We limited our review to the peer-reviewed literature after initial attempts to include unpublished reports and other "gray literature" demon-

TABLE 1. ANALYSIS OF THE EDGE EFFECTS LITERATURE BASED ON PARAMETERS LISTED BELOW, RECORDED FOLLOWING REVIEW OF 215 PAPERS PUBLISHED OVER A 66-YR PERIOD

- Study Type—observational, experimental, theoretical, or modeling
    - Location–country, state/province
    - Focal habitat type
    - Adjacent habitat
    - Edge definition (e.g., is the edge treated as a gradient or separate habitat type)
    - Focal species
- Study design
    - Replication
    - Response variable(s)
    - Explanatory variable(s) measured
- Results and Conclusions

strated a tremendous volume of work of highly variable quality. Inclusion of gray literature would have substantially increased our sample size, particularly in the West, but that literature could not be accessed in any consistent manner, and a haphazard sampling of material would have compromised our analyses. In this article we attempt to present an unbiased review of the peer-reviewed literature, and we invite the reader to critically explore the voluminous gray literature for additional site- and species-specific information on edge effects.

A total of 215 publications were examined for this chapter. Of these, we eliminated from further consideration any field studies that did not explicitly address avian response to edges (for example, studies that employ edge as one of many possible explanatory variables in multivariate analyses of fragmentation effects; see citations in other chapters in this volume). This left us with 125 studies, providing a comprehensive perspective on the development of the edge effects concept in the primary literature, current understanding of edge effects in the context of habitat fragmentation, and the application of this knowledge in the management of avian populations. Of the 125 publications reviewed, 90 presented original research results involving avian subjects (Appendix), and these are included in the analyses presented below. For this subset of the edge literature, we quantified aspects of each study pertaining to the location, focal habitats, species studied, key results, and several related parameters (Table 1). Conceptual and theoretical treatments of edge effects are discussed in subsequent sections of this chapter.

Unlike the nest predation literature (see recent reviews by Paton 1994, Andrén 1995, Hartley and Hunter 1998), the literature on patterns of bird density and diversity with respect to habitat edges has not undergone a recent review. For this reason, we analyze this body of literature in detail. We report the density and species richness response(s) for every treatment considered in each study (Appendix). For multi-year studies, we consider a treatment to show a response if a statistically significant response (increased or decreased density or species richness at edges) was observed in at least one year, and a non-significant trend in the same direction was observed in other years.

GEOGRAPHIC PATTERNS AND RESPONSE VARIABLES

The majority of published studies of edge effects in avian ecology (88%, N = 60) are from the eastern half of North America (Figs. 3, 4a). Furthermore, the West has produced less than half as much research on this topic than has

FIGURE 3. Map of North America showing number of studies addressing edge effects in landbirds.

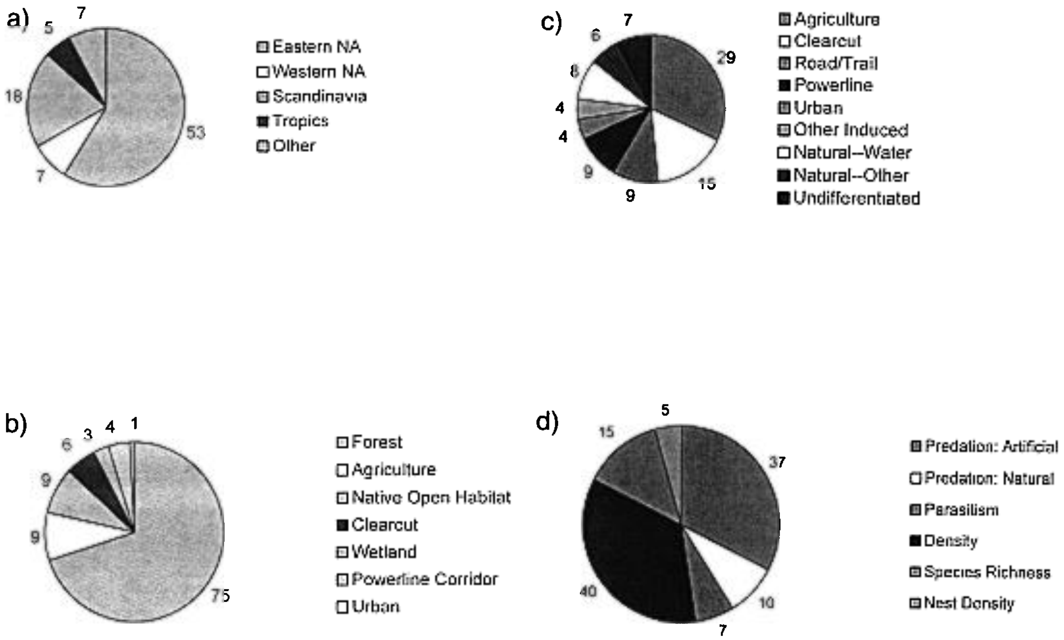


FIGURE 4. The number of edge studies (a) by region, N = 90; (b) by habitat type, N = 90; (c) by adjacent (matrix) habitat, forest edges only, N = 75; (d) by response variable, N = 112 (some studies involved more than one edge type).

Scandinavia, where conditions are, arguably, more similar to eastern North America (Fig. 4a). Clearly, as measured by the number of peer-reviewed publications, studies in Europe and eastern North America have had a tremendous influence on our understanding of edge effects.

Not surprisingly, since forests are the dominant natural habitats in these regions, 73% of all empirical studies focused on forest edges (Fig. 4b), and 33% of these were edges with agricultural habitats (Fig. 4c). Again, there is a geographic bias, as conversion of forested habitats to agriculture (and the reverse) has been a predominant land-use trend in the East and Midwest, whereas edges in western habitats are most often due to timber harvest and a range of factors that degrade, but less often radically transform, native habitats. When this distribution of research effort is viewed in the context of the overall habitat diversity of North America, and when the range of natural and anthropogenic factors that modify habitats and create edges is considered, it is apparent that our understanding of edge effects is largely the product of research focused on a small subset of edge types in eastern, midwestern, and northern European forest edges.

Examination of the response variables measured in empirical edge studies reveals a strong tendency to focus on patterns in species abundance (44% of all studies) and species richness (17%; Fig. 4d). This work highlights patterns in avian distribution near edges but typically does not examine the factors creating the patterns. Fifty-two per cent of all studies quantified rates of nest predation, but of these only 21% looked at natural nests. The remainder manipulated the placement of artificial nests to estimate relative rates in the wild. Nest parasitism, a topic mentioned at least parenthetically in most recent publications on edge effects, was quantified in only 7 of the papers that we reviewed (8%; Fig. 4d). Many other potentially important variables, including competitive interactions, pairing success, movement and dispersal rates, and edge permeability have received scant attention in empirical studies of avian edge effects.

EDGES AND NEST PREDATION

Three recent reviews that have examined the relationship between forest edges and predation have found that, while evidence exists for higher predation rates at edges, this pattern is far from universal (Paton 1994, Andrén 1995, Hartley and Hunter 1998). These reviews addressed not only the question of how frequently predation edge effects occur, but also looked for explanations regarding why some studies found edge effects and others did not. Landscape context was the primary explanatory variable used by all authors, but they drew markedly different conclusions about its importance.

Paton (1994) examined edge effects in nest predation on artificial nests and in both predation and parasitism on natural nests. He found that 10 of 14 studies using artificial nests showed evidence of differential nest predation at edges, compared with 4 of 7 studies of natural nests. Of the 14 studies showing differences, most showed higher predation at edges. Just under half of the 32 studies examined by Andrén (1995) showed higher predation rates near edges, while only 5 of the 13 North American studies examined by Hartley and Hunter (1988) found a difference in predation rates between habitat edges and interiors. These reviews indicate that high nest predation rates occur near edges, but not consistently. Some studies reviewed by Andrén (1995) and Paton (1994) even found lower predation near edges.

In seeking to explain this variable pattern of edge effects, the three reviews draw strikingly different conclusions, though they consider many of the same papers. Paton (1994) concluded that "significant edge effects were as likely to occur in forested as in unforested habitats." Andrén (1995) concluded that predation near edges was more likely in agricultural than in forested landscapes. Hartley and Hunter (1998), who conducted a substantially more rigorous meta-analysis of the association between forest cover and edge effects, found a marginally significant ($P = 0.095$) pattern of higher predation in unforested than in forested landscapes. Unfortunately, the power of their analysis was limited, as they considered only two studies from unforested landscapes.

One possible explanation for the inconsistencies in the findings of these different studies is that Andrén (1995) considered both edge effects and patch size effects in a single analysis, while Paton (1994) and Hartley and Hunter (1998) analyzed edge effects and patch size effects separately. In contrast to their equivocal findings on the relationship between landscape context and the presence of edge effects, both Paton (1994) and Hartley and Hunter (1998) found a very strong relationship between nest predation rate and patch size. This result suggests that Andrén (1995) may have confounded effects by lumping patch size and edge effects in his analysis, and that the strong pattern that he detected could be due to patch size rather than edge effects *per se.*

Another difficulty in interpreting these results is that most of the studies of edge effects on nest predation have been conducted using artificial nests. Hartley and Hunter (1998) used only artificial nest studies in their analysis, while Andrén combined artificial and natural nests. Paton considered artificial and natural nest studies separately, but he found only 7 natural nest studies. The use of artificial nests has been questioned repeatedly in recent years (see Willebrand and Marcstrom 1988; Haskell 1995a,b; Major and Kendal 1996, Yahner 1996), and Haskell (1995a,b) suggested that there is a systematic bias toward increased predation on artificial nests in smaller fragments, a finding that could be especially misleading in studies of predation near edges.

While evidence of increased predation rates near edges does exist, it is not clear that this is a widespread phenomenon, or that it is pronounced in the West. We found only two studies of nest predation in the West, one that used artificial nests (Ratti and Reese 1988) and one that used natural nests (Tewksbury et al. 1998). Neither study found a significant edge effect in nest predation.

PATTERNS IN COMMUNITY ORGANIZATION

For several decades, "edge effects" referred almost exclusively to the increase in species diversity and/or density commonly observed near the edge (Johnston 1947, MacArthur et al. 1962, Giles 1978). A total of 21 studies, with 34 separate treatments, examined density or species richness of the entire bird community (Appendix). Of these, 21 treatments reported higher bird densities near edges, while 10 reported no edge response and 3 showed a decrease. The vast majority of these studies (19 studies, addressing 27 treatments) were conducted in forested habitats, so we restrict our more detailed analyses to these results.

Overall, forest studies showed a strong pattern of higher density at edges but a weaker pattern with regard to species richness. Sixteen treatments recorded higher bird abundance near edges, with 8 showing no significant response and 3 a negative response. Nine treatments found higher species richness at edges, while 10 found no difference, and 2 found a decrease. While an unequivocal pattern of higher bird density and species richness at edges does not emerge from this analysis, it seems clear that, in the recent literature, negative responses to edges are relatively rare and positive responses are common. This could be a manifestation of a general ecological principle (i.e., density and species richness increase at most edges) or the result of a bias in the literature (edge responses in areas where studies have been done are different from those in unstudied areas). Because, as we have shown, there is a strong geographical bias in the literature, this second explanation cannot be ruled out.

All studies (9 studies, 9 treatments) conducted in temperate zone forests that examined total bird abundance at edges between native forests and large anthropogenic openings (matrix = agriculture, clearcut, clearing, anthropogenic grassland; see Appendix) found higher bird densities near the edge. Of the 7 studies that also looked at species richness, 3 found an increase while 4 found no significant pattern. On the other hand, the only study that looked at the difference in overall bird density and species richness along an anthropogenic edge gradient in the tropics found that both decreased near the edge (Lovejoy et al. 1986). Another tropical study, which analyzed edge response by foraging guild, found that two guilds did not differ in abundance and one (insectivores) decreased at the edge (Canaday 1997). These results suggest that even the strongest patterns detected in temperate forests may not generalize well to other habitats and geographic regions.

The effects of linear drivers of habitat fragmentation (roads and powerlines) and natural edges appear to be less consistent. While no studies of road or powerline edges found community-level decreases in avian density, 4 of 7 treatments showed increases and 3 of 7 showed increased species richness. Of the studies that examined natural edges (6 studies, 8 treatments), 3 treatments showed increased density, 4 showed no change, and 1 showed a decrease. Four treatments showed increased species richness at natural edges, with 2 showing no change, and one showing a decrease.

Aside from the suggestion that edge responses may differ between the tropics and the temperate zone, no clear geographical patterns of edge response were evident. No studies from eastern North America recorded decreases in total bird abundance (Fig. 5a) or species richness (Fig. 5b) at edges, but almost as many treatments showed no response in overall bird density (6) as showed an increase (9). As many treatments showed no response in species richness (7) as showed a positive response near edges (7). The only study from western North America had one treatment that showed increased density and species richness at the forest edge and one that showed no change in either variable (Sisk 1992). Two Scandinavian studies showed decreases in density at edges, while 1 reported no change and 2 found increases. We were surprised at the small number of studies that reported on the entire avian community, especially considering the widely held "rule of thumb" associating edges with higher densities and/or species richness. Many of the studies most commonly cited to support this idea examine only part of the bird community present at the study site.

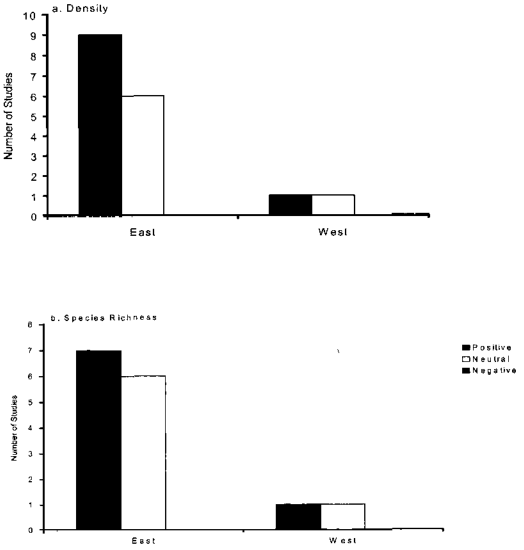


FIGURE 5. Numbers of treatments from studies conducted in eastern and western North America finding positive, negative, or neutral edge responses in total bird density (a) and species richness (b).

Many explanations for the reported trends in avian abundance and diversity near edges have been proposed, and few are mutually exclusive. Few studies have attempted to distinguish among them, and many authors have invoked "edge effects" when discussing any of the myriad influences of habitat fragmentation on disturbance-sensitive species. From this broad range of uses, four general categories of edge effects can be identified:

- *Habitat interspersion.* Species diversity may increase at habitat edges due solely to the proximity of different habitats (Leopold 1933, Giles 1978). At the habitat edge, each community contributes, on average, more than half of its fauna, resulting in higher species diversity at the edge where the two communities mix (MacArthur and MacArthur 1961, Wiens 1989).
- *Resource availability.* Many authors have suggested that birds may utilize more than one habitat type during different activities (e.g., nesting and foraging) or during different life stages. Allocating different activities to the most appropriate habitat may allow some species to maintain higher population densities near edges. It also may provide suitable habitat for species that require more than one habitat type (Kendeigh 1944, MacArthur et al. 1962, Yoakum 1980, Dasmann 1981).
- *Edge as a unique habitat.* Edges may support higher densities of species characteristic of both the adjoining communities, due to in-

creased diversity of the vegetation that typically occurs where two habitats intergrade. Many workers have shown correlations between foliage height diversity and bird species diversity (e.g., MacArthur 1958, Cody 1968, Karr and Roth 1971; but see also Willson 1974). Other studies have shown that floristic composition and the presence or absence of particular plant species are good predictors of both diversity and density of birds (Wiens 1989). Vegetation structure and floristic composition are generally more diverse at edges, so increases in both species diversity and avian density might be expected, even without the addition of edge-dependent species.

- *Interspecific interactions and cascading biotic effects.* Edges, especially those associated with habitat conversion and fragmentation, may permit edge-dependent or habitat-specific species to penetrate some distance into adjacent habitats where they normally do not occur. Their presence can influence the abundance of species in the adjacent habitat, generating cascading effects that penetrate further than the direct environmental changes associated with the edge (Diamond 1978, 1979; Pulliam and Danielson 1991, Fagan et al. 1999). Such secondary effects, including competition, predation, and nest parasitism, are thought to result in the exclusion of forest species from otherwise suitable habitat near habitat edges (Ambuel and Temple 1983, Wilcove et al. 1986, Harris 1988).

SPECIES-LEVEL RESPONSES UNDERLYING COMMUNITY PATTERNS

Each of the definitions of edge effects presented above implies that population densities of some species will change as a function of the distance from the habitat edge. However, few authors have stated explicitly which species they expect to be influenced by habitat edges or how they will respond. In fact, many early studies that support the hypothesis of elevated diversity at edges do not report *which* species contribute to the diverse assemblages found there. Those that do often show that the increase in species richness is due to the addition of common, cosmopolitan, or disturbance-tolerant species, which may mask the loss or decline of sensitive species.

A better understanding of the dynamics in community organization near edges emerges from studies of the responses of individual species near habitat edges (Giles 1978, Dasmann 1981, Harris 1988, Reese and Ratti 1988, Noss 1991, Bolger *this volume*). Many studies have shown that certain species reach their highest or lowest abundance at particular habitat edges (e.g., Kendeigh 1944, Johnston 1947, Hansson 1983, Kroodsma 1984b, Noss 1991, Bolger et al. 1997, Germaine et al. 1997, King et al. 1997). Species that are encountered more commonly near the edge are often termed "edge species" (e.g., Johnson 1975, Giles 1978, Reese and Ratti 1988), and those whose densities are low near the edge are considered to be habitat-interior species (e.g., Brittingham and Temple 1983, Wilcove et al. 1986, Thompson 1993, Bolger et al. 1997). A more quantitative approach to understanding how species respond to habitat edges involves measurement of a species-specific edge response, defined as the pattern of change in population density at incremental distances from the habitat edge (Noss 1991, Sisk and Margules 1993).

Sisk and Margules (1993) proposed a classification scheme for population-level edge responses based on changes in density along a transect from one interior habitat, across the edge, and into the adjacent habitat (hereafter the edge gradient). For some species, the edge itself has no effect on population density (null responses), and changes in density are attributable to differences between the two adjoining habitats. Other species reach their highest density ("edge exploiters") or lowest density ("edge avoiders") near edges (see also Bolger *this volume*). While classification schemes differ among the published studies reviewed here, it is clear that a diversity of responses is manifest in any particular avian community. Four studies from eastern North America show that edge-exploiting responses are generally more common than edge-avoiding responses, with neutral responses (i.e., no edge effect) more common than either in 3 out of 4 studies (Fig. 6a). The small number of Western studies showed similar patterns, except that edge-exploiting responses outnumbered edge-neutral responses (Fig. 6b).

Villard (1998) compared the edge responses of forest-interior neotropical migrants reported in 4 studies from the eastern seaboard stretching from Florida to New Hampshire. He found that there was little consistency in the way that the authors classified responses for the same species. We extended this analysis to all species that occurred in two or more of the studies (Table 2). While there is considerable variability in the responses reported for these species, some patterns do emerge. Most neotropical migrants are edge avoiders, and all disagreements among authors have to do with whether a species shows a neutral response or a positive or negative response; no species is considered an edge-exploiter by one author and an edge-avoider by another. Conversely, species that are not latitudinal migrants showed neutral or edge-exploiting responses.

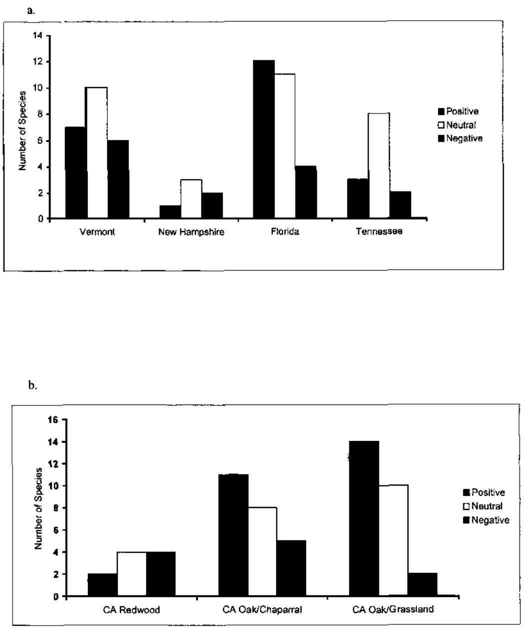


FIGURE 6. Numbers of bird species in four studies showing positive, negative, or neutral responses to habitat edges. Eastern studies (a) were conducted in Vermont (Germaine et al. 1997), New Hampshire (King et al., 1997), Florida (Noss, 1991), and Tennessee (Kroodsma, 1982). Western studies (b) are from California redwood stands (Brand and George *this volume*) and California oak woodlands (Sisk 1992, Sisk et al. 1997).

Again, no species was assigned a positive response by one author and a negative response by another (Table 2). Unfortunately, there are not enough studies of western birds to make similar comparisons, and there is little overlap in species among the few published studies. Three studies from California do, however, seem to show greater variation in the responses of both neotropical migrants and resident species (Sisk et al. 1997, Brand and George *this volume,* Bolger *this volume*).

Ecologists and wildlife managers have often assumed that birds will show consistent, characteristic patterns of habitat selection at edges, even when the adjoining habitats differ in vegetation structure and/or species composition. Implicit in this assumption is the idea that edges of all types share some intrinsic qualities, and that their influence on the distribution of organisms and the composition of assemblages is similar. There is little evidence to support these views. Few studies have measured edge responses at more than one type of edge in a given region, and those that have report differences in the consistency of avian responses at different edge types. Noss (1991) found considerable variation among species and among sites in longleaf pine (*Pinus palustris*) bird communities. Sisk et al. (1997) showed that over half of the breeding birds in oak woodland showed different responses at edges with grassland versus edges with chaparral, and Kristan et al. (in press) found significant site-to-site variation in edge response in several southern California coastal sage scrub bird species. Brand and George (*this volume*) found general consistency at redwood forest edges adjoining habitats as different as logged forest and grassland.

In summary, our examination of empirical studies of edge effects did not identify a simple pattern in avian responses, but it did uncover several important points regarding patterns in community organization and population responses to habitat edges:

- "Edge effects" is an ambiguous term in avian ecology and conservation. Its usefulness is limited by widely varying assumptions that permeate its history.
- Edge effects do not contribute to species diversity in a consistent manner that is easily generalized among sites.
- The abundances of many species change dramatically near habitat edges.
- Edge responses vary markedly among species.
- A given species often responds very differently at different types of edges (but a few studies show consistency).

MECHANISMS UNDERLYING SPECIES-LEVEL RESPONSES

Mechanisms underlying edge effects are many, but few have been adequately investigated (Bolger *this volume*). Sisk and Haddad (2002) hypothesize that several basic driving factors may underlie the broad range of responses typically grouped together under the term "edge effects". These include:

- *Edges influence movement.* Edges may influence behavior, creating barriers to movement even when animals are clearly capable of crossing them (Ries 1998, Haddad 1999). The influence of edges may prevent dispersal through complex landscapes and isolate animals. Sisk and Zook (1996) have shown that "passive accumulation" of migrating birds may generate widely reported increases in density observed near forest edges.
- *Edges influence mortality.* Particularly for habitat interior species, edges may lead to higher mortality in plants and animals. Higher mortality may occur in three different ways. First, edges create greater opportunity for loss

TABLE 2. VARIATION IN SPECIES-SPECIFIC EDGE RESPONSES REPORTED IN DIFFERENT EMPIRICAL STUDIES FROM THE EASTERN USA

Common name	Scientific name	Tennessee (Kroodsma 1984)	Florida (Noss 1991)	New Hampshire (King et al. 1997)	Vermont (Germaine et al. 1997)
Neotropical Migrants					
Yellow-billed Cuckoo	*Coccyzus americanus*	0	+		
Acadian Flycatcher	*Empidonax virescens*	–	–		
Wood Thrush	*Hylocichla mustelina*	0	–		
Hermit Thrush	*Catharus guttatus*		0	–	–
Red-eyed Vireo	*Vireo olivaceus*	0	–	–	–
Black-and-white Warbler	*Mniotilta varia*	+	0		0
Black-throated Blue Warbler	*Dendroica caerulescens*			0	+
Black-throated Green Warbler	*Dendroica virens*			0	+
Hooded Warbler	*Wilsonia citrina*	0	–		
Ovenbird	*Seiurus aurocapillus*	–	0	0	–
American Redstart	*Setophaga ruticilla*			0	0
Summer Tanager	*Piranga rubra*	+	+		
Scarlet Tanager	*Piranga olivacea*	0		0	0
Temperate Migrants					
American Robin	*Turdus migratorius*		0	0	+
Residents					
Red-bellied Woodpecker	*Melanerpes carolinus*	+	0		
Downy Woodpecker	*Picoides pubescens*	0	0		
Carolina Chickadee	*Parus carolinensis*	0	+		
Northern Cardinal	*Cardinalis cardinalis*	+	+		

Note: Results from four studies allowed the classification of 12 species according to their density responses near edges: '+' for edge-exploiting response; '0' for no edge response; '–' for edge-avoiding response; ' ' if not reported (after Villard 1998).

of dispersers into unsuitable habitat. For example, plants with wind-dispersed seeds that are near the edge will lose more of their propagules into unsuitable habitat. Second, edges alter microclimate, including temperature, light, and moisture (Sisk 1992, Chen et al. 1993, Young and Mitchell 1994, Camargo and Kapos 1995). In doing so, edges impact competitive interactions between species. Third, edges provide points of entry for predators and parasites, such as the Brown-headed Cowbird (*Molothrus ater*; Wilcove et al. 1986, Murcia 1995).

- *Edges provide feeding or reproductive subsidies.* From the edge, species may be able to obtain a greater quantity and quality of food resources from each of the habitats that create the edge, leading to positive effects on population sizes (MacArthur et al. 1962, Fagan et al. 1999).
- *Edges define the boundary between two separate habitats,* creating new opportunities for species to mix and interact. By their very nature, edges influence species interactions because they bring into close proximity species that would not normally be present in the same habitat. Species that are brought together at the edge, including predators and prey, new competitors, and mutualists, generate novel interactions and create new communities of species.

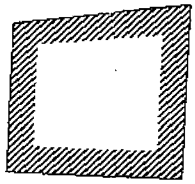
Despite the diversity of hypothesized and documented mechanisms underlying edge effects, surprisingly few studies have attempted to identify the mechanistic basis for edge response and patterns in community organization reported in the literature. Of the 90 field studies considered in this review, most were observational, typically involving some count of individuals or nests in unmanipulated landscapes. The vast majority of experimental studies involved manipulation of artificial nests for the purposes of examining nest predation and parasitism rates; few involved the experimental manipulation of bird habitats (but see Lovejoy et al. 1986).

Forty studies focused on estimates of abundance or species richness, but few examined the mechanisms driving the observed patterns. Donovan et al. (1997) noted that little work has been devoted to exploring the mechanisms underlying observed patterns of edge effects in nest predation and parasitism. This is even more pronounced for studies examining patterns in bird density and species richness. Clearly, the elucidation of mechanisms driving edge effects has lagged far behind pattern identification. Increased attention to the mechanistic drivers underlying edge effects and their relative contribution to observed patterns of distribution and abundance is a fruitful area for future research.

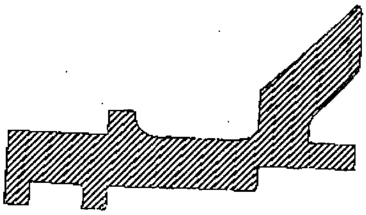
PREDICTIVE APPROACHES TO MODELING EDGE EFFECTS

Despite recent advances in understanding the general consequences of fragmentation, the development of tools for predicting specific impacts has progressed slowly. A growing body of research is demonstrating that edges are often highly influential in determining habitat suitability and population persistence in fragmented landscapes (Robinson et al. 1995a, Donovan et al. 1997, Howell et al. 2000). Like the work focusing explicitly on edges, this landscape-scale research is showing that the importance of habitat edges varies from species to species and from landscape to landscape. Thus, it is increasingly clear that informed habitat management will necessitate the incorporation of our increasing understanding of the role of habitat edges in fragmented landscapes into predictive models that will allow assessment of alternative management options in novel landscapes. Most modeling efforts addressing birds in fragmented habitats have focused on the loss of habitat area and the isolation of remnant patches, typically focusing on a single species (e.g., Thomas 1990, Noon and Sauer 1992, Pulliam et al. 1992). However, models that focus on habitat patches in isolation from matrix and edge effects often prove to be disappointing in management situations (see Saunders et al. 1991). An integrated approach for assessing edge responses and predicting the impacts of increasing edge habitat is needed before the influence of habitat edges can be incorporated into assessments of the effects of habitat fragmentation.

Effective management of habitat edges requires knowledge of population-level responses and a conceptual framework for linking this understanding to spatially explicit information about the landscape. Area-based approaches that treat the edge as an area influenced by adjacent habitats, rather than as a separate habitat type, show some promise for guiding management decisions. In addition, predictive models offer a powerful means for advancing our understanding of the mechanisms that drive observed patterns. The generation of explicit predictions based on empirical measures of species-specific edge responses, followed by field tests and model revision, offer the possibility of more rapid progress in understanding edge effects.



a. Total area 47 ha,
core area 20 ha



b. Total area 39 ha,
core area 0 ha

FIGURE 7. Temple's (1986) original core area model of edge effects used sensitivity to edge as a predictor of habitat use by forest-interior birds. The model assumed that edge effects, in general, penetrate 100 m into a forested patch, dramatically infuencing the "core area" of suitable habitat within a forest patch (contrast panels a, b). The approach motivated a series of efforts that placed edge effects in landscape context and considered edge effects in predictions of the impacts of habitat fragmentation.

Temple (1986) presented a simple, straightforward approach for including edge effects into a patch-based model of avian abundance. He assumed that the effects of nest predators and parasites penetrate about 100 m into remnants of midwestern forest and woodland patches, and that the abundances of species that are "sensitive to fragmentation" would be low or zero within 100 m of the edge patch. He found that linear regressions of species' abundances against the "core area" of the patch—the area greater than 100 m from the edge—were significantly stronger than regressions against total patch area. This idea provided a conceptual foundation for incorporating the effects of edges and patch shape into patch-based approaches to estimating habitat suitability (Fig. 7). Subsequent work relaxed some of the assumptions of the core area model, allowing the distance of edge penetration to vary among species (Temple and Cary 1988) and to vary monotonically with distance from the edge (Laurance and Yensen 1991), adding realism to the approach.

Extension of the core area approach to address all species—those with edge-exploiting as well as edge-avoiding responses—and multiple habitat and edge types, led to the effective area model (EAM; Sisk and Margules 1993, Sisk et al. 1997, Sisk and Haddad 2002). EAM approaches predict species abundances (or other variable of interest) in any number, size, or

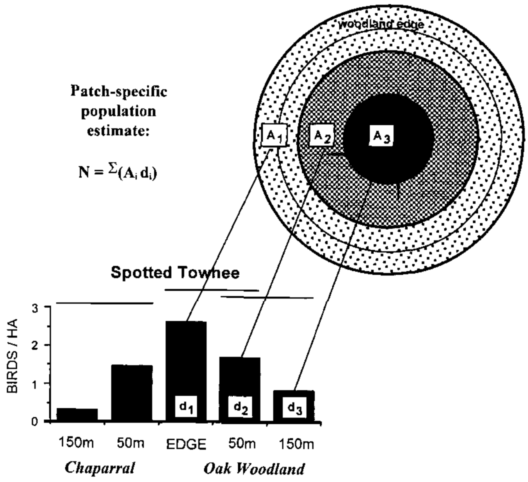


FIGURE 8. Schematic of the effective area model (EAM). Sisk et al. (1997) extended the core area approach to multiple habitat and edge types, using digital habitat maps to describe landscape pattern. The EAM incorporates variation in edge responses among species and at different edge types to estimate the abundances of the breeding bird community in any number of patches of any shape.

shape of habitat patches by projecting density estimates from species-specific edge response curves onto digitized maps of all the habitat patches within the focal landscape. The predicted density of each species within each patch varies with distance from the edge. In the discrete approach illustrated in Figure 8, the patch is divided into sub-regions. These sub-regions correspond to the distance intervals used for field surveys of species abundances, which are used to define species-specific edge responses, illustrated here by the bar graph for Spotted Towhee (*Pipilo maculatus*). Multiplying the area of each sub-region by the corresponding estimate of population density, and then summing the products for all sub-regions, gives a predicted population size for the species in a particular patch (Fig. 8). The degree to which the predicted density differs from predictions that assume equal abundance throughout the patch reflect the importance of "edge effects." Sisk et al. (1997) reported that the EAM performed significantly better than a null model that ignored edge effects and estimated bird abundances based on patch area alone. Other applications of the EAM are presented in Sisk and Haddad 2002.

Several practical considerations influence how the core area and effective area models are applied. First, the spatial resolution of the edge response measured (i.e., the magnitude of the response at various distances from the edge) determines the spatial resolution of the edge effects modeled. Therefore, the sampling design and survey techniques for measuring the edge response should be scaled to the life history characteristics (e.g., territory size, vagility) of the animals being studied. Logistic and methodological limitations often constrain sampling designs somewhat, but the variety of proven methods for sampling avian populations provides flexibility in quantifying edge responses and facilitates the application of these patch-based models to birds operating at different spatial scales. In complex, heterogeneous landscapes, detailed habitat maps reflecting species-specific requirements are needed. Advances in mapping technologies and the application of remotely sensed data to habitat mapping (e.g., Scott et al. 1993, Imhoff et al. 1997), offer promise for rapid and cost-efficient methods for mapping habitats across large regions.

EDGE EFFECTS IN THE WEST: IMPLICATIONS FOR STUDIES OF HABITAT FRAGMENTATION

After 60 years of attention and relatively little progress toward articulating general principles pertaining to edge effects, it might be tempting to conclude that the topic is intractable. Indeed, the early adoption of simplistic rules of thumb regarding habitat edges—for example, that more edge leads to higher diversity—may have led to poor habitat management and stalled progress in identifying the mechanisms underlying edge effects. However, slow progress in the past is not a reason to ignore the compelling reasons for expanding mechanistic and management-relevant research in the future.

Why study edge effects? First, anthropogenic disturbances are rapidly increasing the prevalence of edges in most terrestrial landscapes. This process is sure to continue, and ignoring edge effects will become increasingly debilitating to conservation efforts. Edge effects may compound the effects of habitat loss and the isolation of fragments on the distribution, abundance, and persistence of many sensitive bird species. Second, edges are amenable to management. The area of habitat protected and its location are often the result of societal decisions based on many factors that often lie outside the purview of conservation biologists. However, management of boundaries often is left to the discretion of the manager. Better understanding of the influences of edges on bird populations will lead to more effective strategies for managing habitat fragments. Third, edges are inherently dynamic environments and, therefore, they offer opportunities for studying avian responses to changing landscape pattern.

What do we know? Not nearly enough, but

the numerous studies from eastern North America offer some important lessons for those pursuing studies in western landscapes undergoing fragmentation.

- Our understanding of the many biological phenomena associated with habitat edges is dominated by the description of patterns from eastern forests.
- Western landscapes are, in general, more naturally heterogeneous than their eastern counterparts, and edges are common components in many landscapes (e.g., riparian corridors).
- The relationship between natural heterogeneity and avian sensitivity to the increased prevalence of edge due to habitat fragmentation is not well understood.
- Mechanistic explanations for avian responses near habitat edges are, in general, poorly developed and inadequately tested. Work in the West should pursue mechanistic understanding and predictive capabilities of use to habitat managers.

These lessons, derived from our review of an extensive literature on edge effects and augmented by landscape-scale studies of avian responses to habitat fragmentation, argue that edge effects occur commonly in many habitats, that they are of increasing importance as habitats become more fragmented, and that we currently know too little about what causes them to predict accurately where and to what degree they will influence bird populations. This knowledge should be sufficient to inspire a more focused, and hopefully more fruitful, effort to understand the many driving factors underlying edge effects and to incorporate this knowledge into strategies for avian conservation.

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APPENDIX. SUMMARY OF STUDIES EXAMINING EDGE EFFECTS IN BREEDING BIRDS

Authors	Focal habitat[a]	Matrix[b]	Avian groupings analyzed[c]	Response[d]		Other variables[e]		
				Density	Species richness	Predation	Parasites	Other
		Studies of Density and Species Richness						
Eastern North America								
Anderson et al. 1977	Forest	Powerline	Individual species					
Brittingham and Temple 1983	Forest	Clearing (any opening >0.02 ha.)	Cowbirds	+			√	
Donovan et al. 1997	Forest	Agriculture, old field, wildlife openings				√		
		1. High fragmentation	Cowbirds	–				
		2. Medium fragmentation	Cowbirds	0				
		3. Low fragmentation	Cowbirds	0				
Evans and Gates 1997	Forest	1. Clearcut	Cowbirds	+				
			All other birds	+	0			
		2. Stream	Cowbirds	+				
			All other birds	0	0			
		3. Powerline	Cowbirds	+				
			All other birds	+	0			
		4. Open-canopy road	Cowbirds	+				
			All other birds	+	0			
		5. Closed-canopy road	Cowbirds	+				
			All other birds	0	0			
Ferris 1979	Forest	Highway	All birds	0	+			
Gates and Giffen 1991	Forest	Stream	All birds	+	+			
			Cowbirds	+				
Germaine et al. 1997	Forest	Patch cut	Neotropical edge-open migrants	+				
			Neotropical interior-edge migrants	?				
			Neotropical forest-interior migrants	–				
			Nearctic migrants	0				
			Nonmigrants	0				
			Individual species					
Hawrot and Niemi 1996	Forest	Clearcut, natural openings	All birds	0				
			Individual species					
Hickman 1990	Forest	Nature trail	Individual species					
King et al. 1997	Forest	Clearcut	Individual species					
Lay 1938	Forest	Clearings	All birds	+	+			

APPENDIX. CONTINUED.

				Response[d]		Other variables[e]		
Authors	Focal habitat[a]	Matrix[b]	Avian groupings analyzed[c]	Density	Species richness	Predation	Parasites	Other
Marini et al. 1995	Forest	Agriculture	Ground nesters	–	–	√		
			Understory nesters	0	0			
			Canopy nesters	0	0			
Noss 1991	Forest	Old field, open pine, pine/oak, powerline, marsh	All birds	+				
			Individual species					
Rich et al. 1994	Forest	1. Unpaved road	Forest interior neotropical migrants	0				
			Other forest nesters	0				
			Avian nest predators	0				
			Cowbirds	0				
		2. Paved road	Forest interior neotropical migrants	–				
			Other forest nesters	0				
			Avian nest predators	0				
			Cowbirds	+				
		3. Powerline	Forest interior neotropical migrants	–				
			Other forest nesters	0				
			Avian nest predators	+				
			Cowbirds	0				
Small and Hunter 1989	Forest	1. Powerline	All passerines—Site 1	+	+			
			All passerines—Site 2	0	0			
		2. River	All passerines—Site 3	+	+			
			All passerines—Site 4	0	+			
Yahner 1995	Forest	Anthropogenic openings	Ground-shrub foragers	+				
			Trunk-bark foragers	0				
			Sallier-canopy foragers	–				
Kroodsma 1982[f]	Forest	Powerline	All birds	+				
Kroodsma 1984b[f]	Forest	Powerline	Individual species					
Kroodsma 1987[f]	1. Forest	Powerline	All birds	+	0			
			Powerline birds	+	+			
			Forest birds	0	–			
	2. Powerline	Forest	All birds	0	+			
			Powerline birds	–	–			
			Forest birds	+	+			

APPENDIX. CONTINUED.

Authors	Focal habitat[a]	Matrix[b]	Avian groupings analyzed[c]	Response[d]		Other variables[e]		
				Density	Species richness	Predation	Parasites	Other
Strelke and Dickson 1980	1. Forest	Clearcut	All birds	+	+			
	2. Clearcut	Forest	All birds	0	0			
Kroodsma 1984a	Powerline	Forest	All birds	+				
Best et al. 1990	Agriculture	1. Forest	All birds	+	+			
		2. Herbaceous field	All birds	+	+			
Niemuth and Boyce 1997	Savanna	Fuel breaks (<200 ha.)	Cowbirds	+		√		
			Nest predators	+				
		Wildlife clearings (>1000 ha.)	Cowbirds	+				
			Nest predators	+				
Western North America								
Brand and George 2001	Forest	Natural succession allowed, artificial	Individual species					
Keller and Anderson 1992	Forest	Clearcut	Individual species					
Sisk 1992	1. Forest	1. Chapparal	All birds	0	0			
		2. Grassland	All birds	+	+			
	2. Chapparal	Forest	All birds	+	+			
	3. Grassland	Forest	All birds	+	+			
			Individual species					
Bolger et al. 1997	Shrub, urban	Urban, shrub	Edge/fragment reduced species	–				
			Edge/fragment enhanced species	+				
Scandinavia								
Edenius and Sjöberg 1997	Forest	Mire	All birds	0				
Hansson 1983	Forest	Clearcut	All birds	+				
			Individual species					
Hansson 1994	Forest	Clearcut	All birds	+				
			Individual species					
Helle and Helle 1982	Forest	Shoreline	All birds	–	–			
Thingstad 1995	Forest	Dam development	All birds	–				
Møller 1989	1. Forest	Agriculture	Open-cup ground nesters			√		
			Covered ground nesters	0				
			Open-cup tree nesters	–				
			Hole tree nesters	–				

APPENDIX. CONTINUED.

				Response[d]		Other variables[e]		
Authors	Focal habitat[a]	Matrix[b]	Avian groupings analyzed[c]	Density	Species richness	Predation	Parasites	Other
	2. Agriculture	Forest	Open-cup ground nesters	−				
			Covered ground nesters	0				
			Open-cup tree nesters					
			Hole tree nesters					
Berg and Pärt 1994	Agriculture	Forest	Individual species					
Tropics								
Canaday 1997	Forest	Agriculture, petroleum development	Insectivores	−				
			Frugivores	0				
			Omnivores	0				
Lovejoy et al. 1986	Forest	Clearcut	All birds	−	−			
Other								
Báldi and Kisbenedek 1994	Forest	Agriculture	All birds	+	0			
Cieslak 1992	Forest	Agriculture	All birds	+	+			
Krüger and Lawes 1997	Forest	Anthropogenic grassland	All birds	+	0			
Stroud et al. 1990	Moorland	Conifer plantations	All waders	−				
		Other Studies Reviewed						
Eastern North America								
Bayne and Hobson 1997	Forest	Mixed				√		
Bielefeldt and Rosenfield 1997	Forest	Mixed					√	
Bollinger and Peak 1995	Forest	Mixed				√		
Burke and Nol 1998	Forest	Agriculture						Nest density
Danielson et al. 1997	Forest	Mixed				√		
Fenske-Crawford and Nieme 1997	Forest	Clearcut				√		
Hahn and Hatfield 1995	Forest	Old field					√	
Hannon and Cotterill 1998	Forest	Agriculture				√		Predator type
Hanski et al. 1996	Forest	Clearcut				√		
Keyser et al. 1998.	Forest	Mixed				√		
King et al. 1998	Forest	Clearcut				√		
Linder and Bollinger 1995	Forest	Field				√		
Small and Hunter 1988	Forest	Mixed				√		
Suarez et al. 1997	Forest	Mixed				√	√	Clutch size
Van Horn et al. 1995	Forest	Agriculture						Pairing success
Vander Haegen and DeGraaf 1996a	Forest	Stream				√		

APPENDIX. CONTINUED.

				Response[d]		Other variables[e]		
Authors	Focal habitat[a]	Matrix[b]	Avian groupings analyzed[c]	Den-sity	Species rich-ness	Pre-dation	Para-sites	Other
Yahner et al. 1989	Forest	Mixed				√		
Rudnicky and Hunter 1993	Forest, clearcut	Clearcut, forest				√		
Vander Haegen and DeGraaf 1996b	Forest, clearcut	Clearcut, forest				√		
Yahner and Wright 1985	Forest, clearcut	Clearcut, forest				√		
Gates and Gysel 1978	Forest, agriculture	Agriculture, forest				√	√	Nest density
Strausberger and V. 1997	Forest, grassland	Mixed					√	
Chasko and Gates 1982	Forest, powerline	Powerline, forest				√		Nest density
Özesmi and Mitsch 1997	Marsh	Open water						Nest density
Picman et al. 1993	Marsh	Upland				√		
Fleming and Giuliano 1998	Mixed	Mixed				√		
Pasitschniak-Arts and Messier 1995	Mixed	Mixed				√		
Pasitschniak-Arts and Messier 1996	Mixed	Mixed				√		
Burger et al. 1994	Prairie	Forest				√		
Johnson and Temple 1990	Prairie	Forest				√	√	
Western North America								
Brand and George 2002	Forest	Mixed				√		
Tewksbury et al. 1998	Forest	Mixed				√		
Ratti and Reese 1988	Forest, clearcut	Mixed				√		
Scandinavia								
Berg 1996	Agriculture	Forest				√		
Berg et al. 1992	Bog	Forest				√		
Angelstam 1986	Forest	Open				√		
Huhta 1995	Forest	Road				√		
Huhta et al. 1996	Forest	Mixed				√		
Huhta et al. 1998	Forest	Clearcut				√		
Johnsson et al. 1993	Forest	Agriculture						Cavity use
Kuitunen and Helle 1988	Forest	Mixed				√		Clutch size, lay date
Pösyä et al. 1997	Forest	Lake				√		
Sandström 1991	Forest	Agriculture				√		
Andrén and Angelstam 1988	Forest, agriculture	Agriculture, forest				√		
Tropics								
Arango-Vélez and Kattan 1997	Forest	Agriculture				√		
Burkey 1993	Forest	Road				√		
Latta et al. 1995	Forest	Highway				√		

APPENDIX. CONTINUED.

Authors	Focal habitat[a]	Matrix[b]	Avian groupings analyzed[c]	Response[d]		Other variables[e]		
				Density	Species richness	Predation	Parasites	Other
Other								
Nour et al. 1993	Forest	Agriculture				√		
Santos and Telleria 1992	Forest	Agriculture				√		
Storch 1991	Forest	Agriculture				√		Nest density

[a] Habitats in which edge response was measured.

[b] Habitats bordering focal habitat at which edge response was measured. For studies that combined edges with different matrix habitats together, matrix habitats types are separated by a comma. For studies considering edge types separately, matrix habitats are listed singly with a separate density response for each.

[c] Breakdowns used by authors in analyzing edge effects.

[d] Edge response in bird density and species richness. '+' = density or species richness higher at edge than in interior of focal habitat, '−' = lower at edge, '0' = no significant difference between edge and interior.

[e] Other variables measured by each study; pred = nest predation rate including general nest success calculations, para = nest parasitism rate, other = any other variables measured. √ = variable measured in study.

[f] These three papers are all derived from the same data set. We therefore use only the 1987 results in our analysis, as these represent the most sophisticated analysis.