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A MULTI-SCALE PERSPECTIVE OF THE EFFECTS OF FOREST FRAGMENTATION ON BIRDS IN EASTERN FORESTS

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Abstract. We propose a model that considers forest fragmentation within a spatial hierarchy that includes regional or biogeographic effects, landscape-level fragmentation effects, and local habitat effects. We hypothesize that effects operate "top down" in that larger scale effects provide constraints or context for smaller scale effects. Bird species' abundance and productivity vary at a biogeographic scale, as do the abundances of predators, Brown-headed Cowbirds (*Molothrus ater*), and land-use patterns. At the landscape scale the level of forest fragmentation affects avian productivity through its effect on predator and cowbird numbers. At a local scale, patch size, amount of edge, and the effects of forest management on vegetation structure affect the abundance of breeding birds as well as the distribution of predators and Brown-headed Cowbirds in the landscape. These local factors, along with nest-site characteristics, may affect nest success and be important factors when unconstrained by processes at larger spatial scales. Landscape and regional source-sink models offer a way to test various effects at multiple scales on population trends. Our model is largely a hypothesis based on retroduction from existing studies; nevertheless, we believe it has important conservation and research implications.

Key Words: Brown-headed Cowbirds; eastern forests; edge-effects; fragmentation; landscape; *Molothrus ater*; multi-scale; nest predation; predators; songbirds.

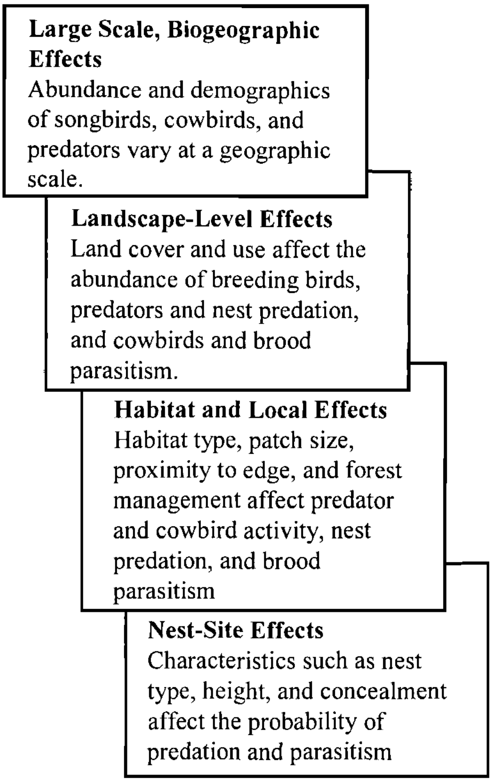
Much recent research has focused on the effects of forest fragmentation on breeding neotropical migrant birds and recent reviews have concluded that forest fragmentation generally results in increased nest predation and brood parasitism (Robinson and Wilcove 1994, Faaborg et al. 1995, Walters 1998). For example, numbers of Brown-headed Cowbirds (*Molothrus ater*), brood parasitism, and nest predation are negatively correlated with the amount of forest cover in landscapes in the midwestern U.S. (Donovan et al. 1995b, Robinson et al. 1995a, Thompson et al. 2000). Enough variation or inconsistency exists among studies, however, that it is difficult to develop a general model of the effects of forest fragmentation on songbirds that addresses spatial scale, accounts for local and regional variation in observed effects, and describes mechanisms for observed effects. Most research has been conducted in eastern forests. Differences in ecological patterns and land use between eastern and western North America, however, has led to speculation that the effects of fragmentation on birds may differ among these regions (George and Dobkin *this volume*).

We have been developing a conceptual model that places the effects of landscape-level forest fragmentation within a spatial hierarchy that ranges from biogeographic or regional effects to local effects (Freemark et al. 1995, Donovan et al. 1997, Robinson et al. 1999, Thompson et al. 2000). Our purpose in developing this model is to provide a synthesis of the current understanding of forest fragmentation effects in eastern landscapes, and to stimulate research that will enhance that understanding in both eastern and western North America. Our model is a simple framework within which factors affecting species viability can be examined. We present the model as a series of hypotheses organized by this framework, and then review key studies that we used to formulate these hypotheses. We present the model as series of hypotheses because it is formed largely by retroduction. Retroduction is the construction of a hypothesis about a process that provides an explanation for observed patterns or facts (Romesburg 1981). Models of this type are often most useful as hypotheses for hypothetico-deductive research (Romesburg 1981), and we review a few studies of this type that test our hypotheses. We do not provide an exhaustive literature review because recent reviews exist (e.g., Robinson and Wilcove 1994, Faaborg et al. 1995, Walters 1998, Heske et al. 2001). We primarily review fragmentation effects at a landscape scale and edge effects at a habitat scale. However, we also discuss effects at larger and smaller scales because of important interactions with edge and landscape effects. For brevity and because of the focus of this volume we focus on biogeographic, landscape, and habitat effects on songbird reproductive success. The context for our review is the eastern deciduous forest, although where possible we make comparisons to western landscapes.

THE MODEL

From a breeding ground perspective, habitat characteristics associated with reproductive success of forest passerines can be evaluated at several spatial scales: (1) *the nest-site scale*—the micro-habitat characteristics directly around the nest or the immediate vicinity of the nest; (2) *the habitat scale*—the features of the habitat patch in which the nest is located; (3) *the landscape scale*—the collection of different habitat patches and the position of a particular habitat within a landscape, the matrix within which the habitat is embedded, and the juxtaposition and proximity of other habitats in the landscape (Freemark et al. 1993); and (4) *biogeographic scales.*

For example, vegetation structure at a habitat scale, or location within a landscape, may be more important than nest site characteristics such as concealment in reducing nest depredation (Bowman and Harris 1980, Leimgruber et al. 1994, Donovan et al. 1997, Burhans and Thompson 1999) or parasitism (Best 1978, Johnson and Temple 1990, Burhans 1997, Morse and Robinson 1999). Furthermore, nest predation or brood parasitism may be related to landscape composition and structure (Robinson et al. 1995a, Donovan et al. 2000, Thompson et al. 2000). Finally, geographic location and abiotic and biotic characteristics at multiple scales can directly impact a population's growth (Hoover and Brittingham 1993, Leimgruber et al. 1994, Thompson 1994, Coker and Capen 1995, Thompson et al. 2000). The essence of our model is that all spatial scales may contribute to the ability of a local subpopulation to replace itself (Sherry and Holmes 1992), but the importance of each may depend on habitat features at other scales or the geographic location within the breeding or non-breeding range. These effects can be arranged in a hierarchy in which larger scale effects provide constraints or context for smaller scale effects (Fig. 1).



Large Scale, Biogeographic Effects
Abundance and demographics of songbirds, cowbirds, and predators vary at a geographic scale.

Landscape-Level Effects
Land cover and use affect the abundance of breeding birds, predators and nest predation, and cowbirds and brood parasitism.

Habitat and Local Effects
Habitat type, patch size, proximity to edge, and forest management affect predator and cowbird activity, nest predation, and brood parasitism

Nest-Site Effects
Characteristics such as nest type, height, and concealment affect the probability of predation and parasitism

FIGURE 1. Conceptual model of factors at multiple spatial scales affecting reproductive success of songbirds. Larger scale factors are hypothesized to be more important determinants of species viability because they provide context or constraints for smaller scale effects.

What types of evidence directly support this model? Evidence of top-down constraints comes from observational, experimental, and meta-analysis studies across eastern North America. Although we provide several examples of correlative evidence for such constraints, we emphasize that experimental and meta-analysis approaches that directly test the top-down constraint hypothesis have been very instructive because they attempt to control for factors operating at other spatial scales. For example, we tested the hypothesis that landscape effects are more significant than local edge effects, and that edge effects are dependent on landscape context, in a rigorously-designed, large-scale, randomized field experiment. We found strong evidence that edge effects in nest predation are dependent on landscape context, and that landscape context is a better predictor of cowbird abundance than any other local-scale affect measured (Fig. 2; Donovan et al. 1997). In landscapes with <15% forest, predation was high in forest edge and interior; at 45–55% forest cover, predation was high in forest edge and low in forest interior; and at >90% forest cover, predation was low in forest edge and interior. Cowbird abundance was much greater in landscapes with high levels of forest fragmentation than those with low levels of fragmentation (Fig. 2). While we could not randomly assign landscape treatments in this study (because the landscape patterns already existed), study sites were randomly selected from a three-state area. As a result, we believe these results allow strong inferences for at least Missouri, Illinois, and Indiana. The results of this research were also confirmed by a meta-analysis of nest depredation studies in which researchers compared the landscape context for studies that documented edge effects on predation patterns with those that failed to find edge effects (Bayne and Hobson 1997, Hartley and Hunter 1998).

We believe that these large-scale analyses are

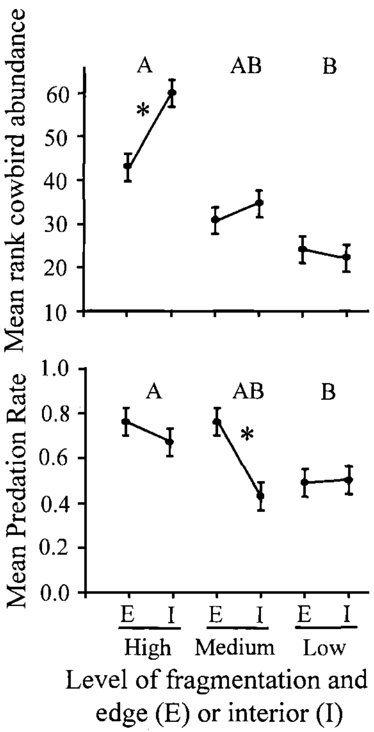


FIGURE 2. Effects of landscape level of fragmentation and local edge effects on nest predation and cowbird abundance in the midwestern United States. Fragmentation levels were measured as the amount of forest cover and were: high, < 15% forest; medium, 45–55% forest; and low, > 90% forest. Edge (E) and interior (I) treatments were 50 m and > 250 m from forest edge, respectively. Levels of forest cover with different letters, and edge and interior treatments with an asterisk are significantly different (ANOVA, $P < 0.05$). Data and figures adapted from Donovan et al. (1997).

critical for understanding how forest fragmentation impacts songbird populations. Although artificial nest experiments at large spatial scales may provide some insights, our hypothesis that larger scale effects provide constraints or context for smaller scale effects depends on observations of nesting success at numerous locations across a species' range. Obviously, collection of these data is not an easy task, and significant advances will likely be made through large-scale collaborations (e.g., Robinson et al. 1995a), large-scale research programs with standardized methodology (e.g., BBIRD; Martin et al. 1997), or through meta-analyses (e.g., Hartley and Hunter 1998, Chalfoun et al. 2002). We have focused on direct measures of nesting success, nest predation, and predator abundance; however, we recognize that indirect measures will be necessary and provide insight at large spatial scales (e.g., Project Tanager; Rosenberg et al. 1999).

LARGE-SCALE, BIOGEOGRAPHIC EFFECTS

Hypothesis: Breeding birds exhibit geographic patterns in their demographics. These are in part the result of geographic patterns in the distribution of predators and cowbirds, and provide the context for smaller scale effects and can affect local reproductive success.

PREDATOR DISTRIBUTION

Predator abundance and species richness vary across North America. Levels of nest predation could be higher where the total abundance and diversity of predators is higher. For example, Rosenberg et al. (1999) documented biogeographic patterns in predator communities as part of Project Tanager. Tanagers (*Piranga* spp.) were exposed to different combinations of predators across their range, and predators responded differently to forest fragmentation. The highest incidence of the predators they surveyed occurred in the Midwest. General patterns in the distribution of avian predators can be generated from Breeding Bird Survey (BBS) data (Sauer et al. 1997). Detecting biogeographic patterns in nest predation related to predator abundance or diversity will be difficult because of the large number of potential nest predators and variation in their distributions across North America. Further complicating these patterns is the interaction between diversity and abundance; even in areas of low predator diversity a single predator may be very abundant.

BROWN-HEADED COWBIRD DISTRIBUTION

Cowbirds demonstrate strong geographic patterns in abundance; therefore, the potential effects of fragmentation or habitat effects are constrained by this larger-scale effect. More simply put, in regions of the country where cowbirds are rare it is unlikely that fragmentation or local factors will have a strong effect on parasitism levels.

The strongest evidence of this geographic effect comes from BBS data. A distribution map generated from BBS data shows a general pattern of high abundance of cowbirds in the Great Plains and decreasing abundance with distance from the Great Plains (Sauer et al. 1997). Thompson et al. (2000) examined patterns from the BBS data by regressing mean statewide cowbird abundance on distance from the center of their range in the Great Plains and the percent of forest cover in that state. Mean statewide cowbird abundance was negatively related to forest cover in a state and a state's distance from the center of the cowbird's breeding range ($R^2 = 0.67$). Regression coefficients for distance to center of range and forest cover were both significant. However, the partial correlation of distance to center of range with cowbird abundance was greater than that for forest cover and cowbird abundance. While both partial correlations were significant, the effect of distance to the center of the range was stronger and provides some indication of the importance of biogeographic constraints. Additional evidence of this effect is seen in parasitism levels. Wood Thrush (*Hylocichla mustelina*) parasitism levels decrease from Midwest to Mid-Atlantic to New England (Hoover and Brittingham 1993; see also Smith and Myers-Smith 1998).

LANDSCAPE-LEVEL EFFECTS

Hypothesis: Nest predation and cowbird parasitism increase with forest fragmentation at the landscape scale. Predation and parasitism is greater in fragmented landscapes because of a positive, numerical response by predators and cowbirds that is the result of increase in the availability and interspersion of food, hosts, or other resources.

A landscape is a heterogeneous mosaic of habitat patches in which individuals live and disperse (Dunning et al. 1992), usually ranging in size from a few to hundreds of square kilometers. Most research on landscape-level effects and fragmentation has occurred in the last decade; understanding the logical importance of these factors required a major shift in our concepts of habitat relationships. Biologists, however, have been documenting the distribution of forest passerines in relation to habitat and habitat-patch characteristics for literally decades (e.g., Robbins et al. 1989b; reviewed by Freemark et al. 1995), often using the MacArthur and Wilson (1967) model of island biogeography as a guiding framework (reviewed in Faaborg et al. 1995). Patch size, patch shape, and interpatch distances, as well as forest type, have important effects on bird community composition. However, there is ample evidence to suggest that these local patterns are driven in part by habitat characteristics at the landscape scale, and also vary regionally. Most investigators of fragmentation effects recognized that habitat fragments differed from true islands because the matrix between the fragments was not ocean, but was a different habitat that supported its own set of species. The inclusion of "edge" species in counts on fragments was certainly one form of recognition that effects from the surroundings of the study site could be important. However, to truly understand all the effects of landscape-level processes upon forest birds we needed to study a variety of landscapes, as opposed to a variety of patches.

Patterns of Land Cover and Their Effects on the Abundance of Predators and Nest Predation

Land cover can significantly influence the number and diversity of predators, as well as constrain the importance of more local-scale habitat factors such as patch size, vegetation structure, or distance to edge effects on nest predation. We begin by reviewing the main effects of landscape pattern, and then discuss how landscape factors potentially constrain more local-scale effects on nest predation. Detection of this constraint, however, may be difficult because predators throughout North America vary greatly in habitat use, foraging behavior, and how they collectively contribute to observed nest predation patterns in forest passerines (e.g., Gates and Gysel 1978, Andrén and Angelstam 1988, Yosef 1994, Tewksbury et al. 1998, Marzluff and Restani 1999, Dijak and Thompson 2000).

Robinson et al. (1995a) and Donovan et al. (1995b) were the first to use empirical data from real nests to relate nest predation to forest fragmentation at a landscape scale. They measured many landscape variables but used the percent of forest cover within a 10-km radius as a simple measure of forest fragmentation and examined its correlation with daily nest predation. Correlations for all nine species were in the predicted direction, three correlations were significant ($P < 0.05$), and two additional species had P-values between 0.05 and 0.20. A combined probabilities test on all nine species indicated the overall effect of percent forest cover was significant ($P < 0.02$). Here we present data points and regression lines for two of the species with significant effects, and two with marginally significant effects (Fig. 3). For all these species the highest nest predation rates occurred in landscapes with less than 40% forest cover. Given the high variability in nest predation rates over both time and space, we believe these results are indicative of an important relationship even though some of the correlations were not statistically significant by the conventional criterion.

Two studies have since corroborated the hypothesis that nest predation increases with forest fragmentation in eastern forests. In a rigorously designed observational study, Donovan et al. (1997) tested hypotheses concerning edge and landscape effects on nest predation and parasitism. They randomly selected 18 landscapes from three states with high, moderate, or low levels of fragmentation and determined predation rates of artificial nests in interior and edge habitat.

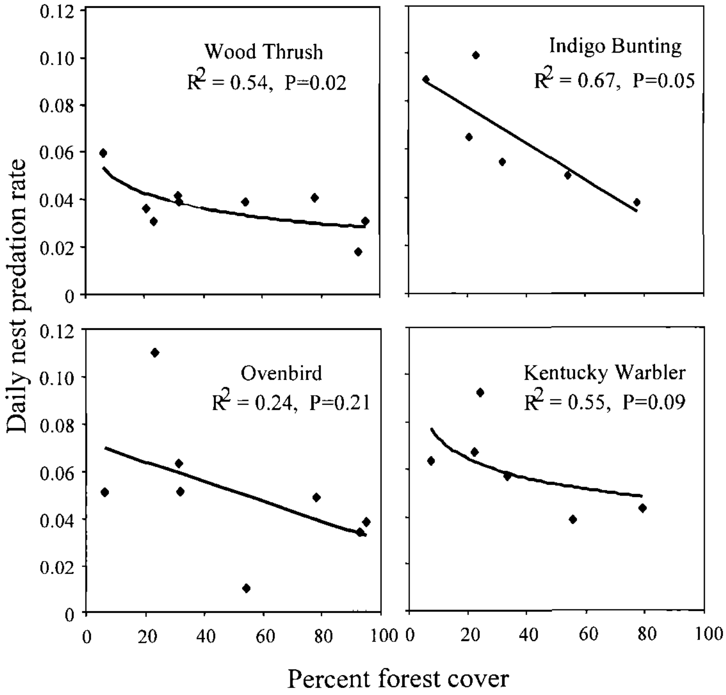


FIGURE 3. Relationship of daily nest predation to the amount of forest cover in landscapes defined by a 10-km radius in the Midwestern United States. Data are from Robinson et al. (1995a).

Predation rates increased with forest fragmentation, and fragmentation (landscape) effects overwhelmed local edge effects (Fig. 2). Hartley and Hunter (1998) conducted a meta-analysis of a set of artificial nest experiments and showed that predation rates increased as forest cover decreased at 5-, 10-, and 25-km scales of forest cover. Both Donovan et al. (1997) and Hartley and Hunter (1998) addressed factors at multiple scales by investigating the interaction between local edge effects and landscape fragmentation effects, and we discuss this later under edge effects.

Many of the previous studies used percent forest cover in a defined landscape as the independent variable. Most, however, used this measure because it was a convenient index of fragmentation, and hypothesized predation and parasitism were high in fragmented landscapes as a result of increases in the abundance of generalist predators and cowbirds (Donovan et al. 1995b, Robinson et al. 1995a, Thompson et al. 2000).

Tewksbury et al. (1998) reported levels of predation at real nests increased with higher landscape-levels of forest cover. While their results are contrary to our hypothesis and findings for eastern forests, nevertheless they found a landscape effect on nest predation. They believed the primary predator in their landscape was the red squirrel (*Tamiasciurus hudsonicus*), and red squirrels were more abundant in heavily forested landscapes. We believe this difference can be explained by our overall model as a difference in predator communities resulting from biogeographic and habitat differences in predator communities. Another study (Friesen et al. 1999) found relatively high nesting success in a highly fragmented landscape in Ontario, but it is not possible to conclude if this difference was due to annual variation, biogeographic context, or a lack of generality of the fragmentation effect.

The effects of landscape composition on predator abundance and distribution have received much less attention than patterns in nest success (Chalfoun et al. 2002). Raccoons (*Procyon lotor*) and opossums (*Didelphis virginiana*) reach their highest densities in highly fragmented landscapes (Andrén 1992, Dijak and Thompson 2000), potentially because their distributions are associated with developed and agricultural habitats that are interspersed with forest habitat. In eastern North America Blue Jays (*Cyanocitta cristata*) are significantly more abundant in highly fragmented landscapes with <15% forest cover than in landscapes with moderate or high forest cover (T. M. Donovan, unpubl. data). Rosenberg et al. (1999) surveyed occurrence of some potential nest predators along with tanager species; they generally found positive relationships between predators and fragmentation, but responses were often region or species specific. Abundance of some other predator species, however, may not be affected by forest patterns at a landscape scale, but by more local habitat effects such as edge.

PATTERNS OF LAND COVER AND THEIR EFFECT ON THE ABUNDANCE OF COWBIRDS AND BROOD PARASITISM

Landscape considerations seem logical for cowbirds because cowbirds utilize different habitats for feeding and breeding activities in the midwestern U.S. (Thompson 1994). Cowbirds generally feed in open grassy or agricultural areas, whereas breeding resources (hosts) are often distributed in forested areas (Rothstein et al. 1984, Thompson 1994, Thompson and Dijak 2000). Telemetry studies in Missouri and New York show that although feeding and breeding resources can overlap spatially, cowbirds move between them to optimize the use of each resource (Thompson 1994, Hahn and Hatfield 1995). In Missouri, female cowbirds tend to parasitize nests in host-rich forests in the early morning and move to open grassy or agricultural areas to feed as the day progresses (Thompson 1994, Morris and Thompson 1998, Thompson and Dijak 2000). Also, cowbirds are common in hayfields and mowed roadsides in the White Mountains of New Hampshire, but do not occur in adjacent forest even though permanent openings and clearcuts exist in the forest (Yamasaki et al. 2000). Cowbirds are also more abundant along corridors such as roads that include mowed grass, than in forest interior in New Jersey (Rich et al. 1994). While the specific habitats used differ, the same landscape relationships between feeding and breeding habitat exist in western landscapes (Rothstein et al. 1984). The probability that a cowbird occurs in a forest, therefore, depends at least partly upon the probability that a feeding area is nearby. As areas become more forested, cowbird breeding opportunities may increase but feeding opportunities may decline. Hence, in heavily forested environments such as the Missouri Ozarks, cowbird densities are low and parasitism rates of forest birds have been recorded in the 2–4% range (Clawson et al. 1997). In contrast, fragmented agricultural regions can support massive cowbird populations that attack the limited number of forest breeding birds, resulting in parasitism rates approaching 100%, with high rates of multiple-parasitism in a single nest (Robinson 1992). In this case, cowbirds are probably not food limited but may be constrained by the number of available host nests.

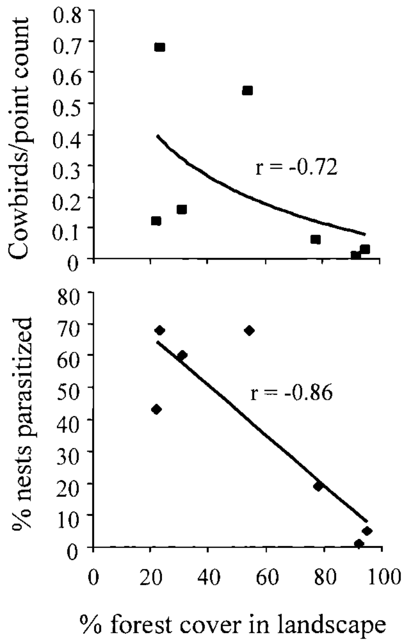


FIGURE 4. Correlation of the amount of forest cover in a 10-km radius with cowbird relative abundance and level of brood parasitism in the Midwestern United States. Data and figures are adapted from Thompson et al. 2000.

Cowbird abundance and levels of parasitism are closely correlated with landscape statistics reflecting the amount of forest fragmentation, the percent of forest cover, and the amount of potential feeding habitat (agricultural land uses) in the landscape. For example the number of cowbirds and level of brood parasitism are both highly negatively correlated with the amount of forest cover in a 10-km radius (Fig. 4). Landscapes have been defined by 5- to 10-km radii in these studies (Robinson et al. 1995a, Donovan et al. 2000, Thompson et al. 2000), which relates well to the distances most cowbirds commute between breeding and feeding areas (<5 km; Thompson 1994, Thompson and Dijak 2000).

Hochachka et al. (1999) combined numerous data sets from across the United States to test the generality of the midwestern pattern at two different spatial scales. They found that increasing amounts of forest cover within 10 km of study sites was correlated with reduced parasitism rates across the continent. In contrast, when they analyzed the data using forest cover within 50 km of the study site, they found that increasing forest cover resulted in slightly increased parasitism rates in sites west of the Great Plains.

Although there are still details that we do not understand, it appears quite clear that there are landscape-level effects on cowbird densities that affect parasitism rates throughout the range of the Brown-headed Cowbird.

We have suggested that the importance of landscape composition in limiting cowbird numbers is constrained by biogeographic location. Is there evidence that landscape composition constrains the importance of local-scale effects such as host density, nest concealment, or other factors? Several studies suggest that cowbirds select habitats with high host densities (Verner and Ritter 1983, Rothstein et al. 1986, Thompson et al. 2000). However, this relationship may depend upon whether landscapes offer both breeding and feeding opportunities for cowbirds. In Missouri, cowbirds are more abundant in fragments than in contiguous forest with a comparatively greater abundance of hosts (Donovan et al. 2000). We found evidence that cowbird and host abundances were correlated in fragmented landscapes, but not in contiguous forest landscapes, suggesting that landscape composition may constrain the influence of local host abundance on local cowbird abundance. If food or host resources are scarce at the landscape scale, local habitat characteristics may not explain either cowbird abundance or parasitism levels.

Landscape composition may also constrain the importance of local-scale habitat features such as edge or patch size in determining cowbird numbers and parasitism levels. For example, in a heavily forested landscape in Vermont (94% forest cover), cowbird distribution at the patch level was best explained by examining one local-scale habitat characteristic (patch area) and two landscape-scale habitat characteristics (distance to the closest opening and the number of livestock areas [known feeding areas] within 7 km of the patch; Coker and Capen 1995). Similarly, in Missouri the distribution of cowbirds is not as well correlated with patch level statistics such as area or the ratio of perimeter to area, but by landscape-level measures that encompass the known daily movements of cowbirds (Donovan et al. 2000).

HABITAT-SCALE EFFECTS

Hypothesis: Habitat-scale factors affect the probability a nest is depredated or parasitized because of effects on predator and cowbird abundance and activity patterns or nest detectability. The strength of these effects depends on the biogeographic and landscape context.

Within a given biogeographic and landscape context, nest predation and brood parasitism should be related to habitat effects. Species demographics vary among habitats as a reflection of habitat quality. The question of interest here is whether there are consistent features or processes at the habitat scale, or interactions with landscape and biogeographic processes that elevate predation and parasitism. Several possibilities of habitat effects are patch size, proximity to edge, forest management, and nest concealment. These effects have been widely studied, yet there are substantial gaps in our knowledge and inability to explain known effects within a conceptual model. Recent reviews (Martin 1993, Paton 1994, Robinson and Wilcove 1994, Faaborg et al. 1995, Heske et al. 2001) have addressed these topics to various degrees. Here we address edge and forest management effects and how they fit within our general model.

EDGE EFFECTS

Edge effects are not uniform within or among regions (cf. Bolger *this volume*). Many studies show no edge effects or only such effects very close (<50 m) to edges (Paton 1994, Hartley and Hunter 1998). Parasitism levels remain high in forest far from edge in some landscapes (Marini et al. 1995, Thompson et al. 2000), and in at least one landscape parasitism in forest declined gradually from 70% to 5% over a gradient of 1500 m from an agricultural edge (Morse and Robinson 1999).

At least four hypotheses have been suggested for higher predation rates near edges: (1) predators may be attracted to edges because of abundant prey (a functional response; e.g., Gates and Gysel 1978, Ratti and Reese 1988); (2) predator density may be greater near edges than in forest interiors (a numerical response; e.g., Bider 1968, Angelstam 1986, Pedlar et al. 1997); (3) the predator community may be richer near edges (Bider 1968, Temple and Cary 1988, Marini et al. 1995); and (4) predators may forage along travel lanes such as edges (Gates and Gysel 1978, Yahner and Wright 1985, Small and Hunter 1988, Marini et al. 1995).

Results of edge-effects studies have been inconsistent and comparisons among studies have been confounded by lack of experimental control of landscape or habitat context, differences in predator communities, and methodological biases. Problems associated with artificial nests exist (e.g., nest appearance, lack of parental and nestling activity), but even the types of eggs used in artificial nests may bias results. Large eggs (i.e., quail or chicken) exclude predation by some small predators and predation rates are greater when small eggs are used (Haskell 1995a, DeGraaf and Maier 1996). Lack of a mechanistic approach that addresses hypotheses for why predation should be higher near edges has also hampered research. A more mechanistic approach requires studies of predator activities or abundances, not just nest predation patterns.

Equally variable are the results of nest placement studies (i.e., ground vs. shrub/elevated nests). Major and Kendal (1996) reported higher predation at elevated nests in six studies, higher predation at ground nests in four studies, and equal predation rates in three studies. Ground nests containing Japanese Quail (*Coturnix* spp.) and plasticine eggs exhibited increased predation along farm edge and interior in Saskatchewan, but there were no detectable differences in predation rate between ground and shrub nests in logged edge, in logged interior, or in contiguous forest (Bayne and Hobson 1997). Although two studies in the northeastern U.S. did not detect any difference in predation rates between ground and shrub nests (Vander Haegan and DeGraaf 1996, Danielson et al. 1997), DeGraaf et al. (1999) found a strong placement effect (high predation on ground nests) using small eggs, as did Marini et al. (1995).

Our perspective on edge effects is from studies in eastern forests that largely investigated predation of forest bird nests by medium sized mammals such as raccoons and opossums, and corvids such as Blue Jays and American Crows (*Corvus brachyrhynchos*). Based on our studies and others, we offer two predictions that may help account for the variability among previous studies.

Edge effects are dependent on landscape and habitat context

The importance of landscape context is emerging as perhaps one of the few generalities that can be made concerning edge effects. Our hypothesis is that the occurrence of local edge effects is dependent on landscape composition and pattern because of dependence of predators and cowbirds on landscape-level factors. Some evidence exits to support this hypothesis. Edge effects tend not to exist in mostly forested landscapes (Heske 1995, Marini et al. 1995, Bayne and Hobson 1997, Hartley and Hunter 1998, DeGraaf et al. 1999, Chalfoun et al. 2002). Some level of forest fragmentation is necessary to support high numbers of generalist predators in eastern forests. At moderate levels of fragmentation elevated predation rates will be limited to edges because predators depend on agricultural habitats or human settlements. At extreme levels of fragmentation all forest habitat is within close proximity to these habitats and predation is high throughout the forest. We believe edge effects are a result of increases in abundance of predators due to landscape effects (fragmentation) and activity patterns of predators in fragmented landscapes (Andrén 1995, Chalfoun et al. 2002).

As previously discussed, Donovan et al. (1997) directly tested this hypothesis with a rigorous field experiment using artificial nests, and found strong support for it. Hartley and Hunter (1998) detected the same effects in a meta-analysis of artificial nest studies. In a different meta-analysis Chalfoun et al. (2002) determined that predator responses to edges, patch size, or fragmentation were not independent of landscape context. Predator abundance or activity was related to edge, patch area, or fragmentation in 66.7% of tests when adjacent land use was agricultural, 5.6% when forest, 16.7% when grassland, 5.6% when clearcut forest.

In addition to the effect of landscape context on predator abundance, landscape and habitat contexts also affect the species of predators present. The variability in results among studies of egg predation may reflect differences in nest predator communities or the abundance of particular species in study areas (e.g., Picman 1988). For example, in New England Blue Jays and raccoons were predominant predators of artificial nests in suburban forests, whereas fishers (*Martes pennanti*) and black bears (*Ursus americanus*) were important in extensive forest (DeGraaf 1995, Danielson et al. 1997), and no avian nest predators were detected in the interiors of extensive forest (DeGraaf 1995).

Attempts to identify egg predators include characterizations of predation remains of real eggs (Gottfried and Thompson 1978; but see Marini and Melo 1998), impressions in plasticine (Bayne et al. 1997) and clay eggs (Donovan et al. 1997), hair catchers (Baker 1980), and remotely triggered cameras (DeGraaf 1995). The most promising technique, however, may be the use of subminiature video cameras with infrared illumination at real nests (Thompson et al. 1999, Bolger *this volume*). For example, F. Thompson and D. Burhans (pers. comm.) used this technique and determined 85% of nest predation events in old fields were by snakes, whereas 60% of predation events in forests were by raccoons.

Not all edges are the same

We suggest that negative edge effects are most likely to occur where land-use patterns or topography concentrate activities of predators, and are therefore a functional response by predators. Edge effects are most likely to occur where forest abuts habitats that provide key resources for predators. Agricultural edges generally have stronger edge effects than other types of edge (e.g., regenerating forest, grassland) on nesting success (Hanski et al. 1996, Hawrot and

Neimi 1996, Darveau et al. 1997, Hartley and Hunter 1998, Marzluff and Restani 1999, Morse and Robinson 1999; but see King et al. 1996, Suarez et al. 1996) and on predators (Chalfoun et al. 2002). Differences in results among studies likely are due at least partly to differences in habitat use among predators.

In one of the few studies of predator distributions relative to edges, Dijak and Thompson (2000) showed that raccoons respond differently to different edge types. Raccoon activity was significantly greater in forest adjacent to agricultural fields and riparian areas than in forest adjacent to roads, clearcuts, or forest interior. Studies of raccoon foraging behavior show that the degree of nest cover is much less important than local habitat heterogeneity in preventing depredation (Bowman and Harris 1980). In Illinois Blue Jays used edges differently and preferred gradual shrubby edges (J. Brawn, unpubl. data). Avian predators were more abundant in forest-dividing corridors composed of shrub-sapling vegetation than grass in New Jersey (Rich et al. 1994). Heske (1995), however, found no significant difference in predator activity adjacent to and >500m from edges. Recent work in New England oak forests showed that six species of small mammals represented 99% of captures at both forest edge and interior and their abundance and nest predation rates did not differ between edge and interior (DeGraaf et al. 1999). We believe these differences in edge effects are a result of differences in predator species, type of edge, and landscape context.

SILVICULTURAL PRACTICES

Silvicultural practices such as tree harvest and regeneration of stands (habitat patches) dramatically affect habitat scale characteristics. Bird communities can change greatly in response to these practices, and balancing the needs of species with diverse habitat needs in managed forests is a challenge for land managers and planners (see review by Thompson et al. 1995). Here we focus on two aspects of silvicultural practices that are related to concerns for forest fragmentation: fragmentation of old forests by young forests, and creation of edges between old and young forests.

Fragmentation of mature forest by young forest

Fragmentation of mature forest by young forest created by timber harvest has raised conservation concerns because of the loss of mature forest habitat and potential fragmentation effects. Both even-aged forest management and uneven-aged forest management result in changes in the bird community (Thompson et al. 1992, Annand and Thompson 1997, Robinson and Robinson 1999). These changes in the bird community can be interpreted as good or bad depending on management objectives. Habitat needs of forest breeding birds need to be addressed by identifying conservation objectives and then evaluating the effects of land management practices on these. Young forests in the East provide habitat for at least some species acknowledged as management priorities (e.g., Kirtland's Warbler [*Dendroica kirtlandii*], Prairie Warbler [*Dendroica discolor*], Golden-winged Warbler [*Vermivora chrysoptera*]); therefore the needs of early and late successional species need to be addressed in forest management plans.

We are aware of no evidence in eastern forests that fragmentation of mature forest by young forest creates the type of negative fragmentation effects that fragmentation by agricultural or developed land uses do. We have suggested that cowbirds and generalist predators benefit from interspersion of agricultural and developed land use in forests because they provide rich food sources, but this would not seem to apply to young forests. For example, in extensively forested northern New England, predation rates on artificial ground and shrub nests were not different among timber size-classes (DeGraaf and Angelstam 1993). Likewise, predation rates on artificial ground and shrub nests were similar in managed and reserved large forest blocks (DeGraaf 1995).

Edge effects between mature and young forest

Not many studies have directly addressed edge effects in managed eastern forests. The evidence for edge effects between mature forest and recently harvested stands is highly variable and suggests results vary locally. In a study of Ovenbird (*Seiurus aurocapillus*) reproductive success in northern New Hampshire in relation to clearcutting (King et al. 1996), nests, territories, and territorial males obtaining mates were equally distributed in edge (0–200 m) and interior (201–400 m) mature forest. Nest survival was higher in forest interior in year 1, but not in year 2. The proportion of pairs fledging at least one young, fledgling weight, and fledgling wing-chord did not differ between edge and interior in either year, nor did the number of young fledged per pair. In another study artificial nests were placed in edge areas (0–5 m from edges) and interior areas (45–50 m from edges) adjacent to clearcuts and groupcuts. The probability of a nest being depredated was higher in edge than interior, and was independent of nest concealment, nest height, or whether adjacent to clearcuts or group-selection cuts (King et al.

1998). In Illinois forest predation of Kentucky Warbler (*Oporornis formosa*) nests was not related to clearcut edges (Morse and Robinson 1999). Nest predation, however, was significantly higher in clearcuts than adjacent older forests, suggesting differences in vegetation structure were important while edge was not. Edge effects can differ among species nesting in the same habitat patch as well. Woodward et al. (2001) determined that nest success of songbirds nesting in regenerating forests and cedar glades varied with distance to mature forest edge, but that patterns were different among species and did not generally increase monotonically with distance from edge.

Given that edge effects seem to vary locally it is important to remember the top down nature of our model. Landscape level fragmentation of forests by habitats that elevate predator and cowbird numbers is likely a more important determinant of nest success at a population level than are local edge effects. While some studies have demonstrated edge effects, no studies have shown a population-level effect on viability.

POPULATIONS ARE STRUCTURED AS SOURCES AND SINKS

Hypothesis: Top-down spatial constraints limit reproductive success in some fragmented landscapes in the Midwest to the point where populations in such landscapes will either decline to extinction or will persist as part of a larger, source-sink system The presence of sink populations may or may not be a detriment to the larger population, depending on the amount of sink habitat in the landscape and to what degree individuals select sink habitat for breeding.

AT A POPULATION SCALE, SINKS EXIST IN HIGHLY FRAGMENTED HABITATS

Source-sink theory (Pulliam 1988) has become a popular framework for describing the population dynamics of organisms that are affected by habitat fragmentation. Pulliam (1988) used models based on births, immigration, deaths, and emigration (BIDE models; Cohen 1969, 1971) to describe geographic subpopulations that are connected by dispersal. All subpopulations contribute individuals that make up the greater population, or the entire source-sink system. At equilibrium, a subpopulation is a source when $B > D$ and $E > I$; and is a sink when $B < D$ but $E < I$. The greater population is at dynamic equilibrium (not changing) when B (all the births) + I (all the immigrants from outside the greater population) − D (all the deaths) − E (all the emigrants that leave the greater population) = 0. If habitat fragmentation subdivides populations into more or less independent breeding subpopulations, then source-sink structure may be an appropriate demographic model.

Is there any evidence that forest passerines exhibit source-sink population structure that is linked to the degree of habitat fragmentation? Several field studies document that reproductive success of neotropical migrant birds varies across a species' range (Probst and Hayes 1987, Robinson et al. 1995a), but few studies examine the interaction of subpopulations from a source-sink viewpoint. One must know the BIDE parameters of each subpopulation to evaluate source-sink dynamics. Measurement of these parameters is extremely field intensive and potentially unachievable with current techniques because of the dispersal capabilities of birds. Surveys of bird abundance may not be capable of establishing source-sink status (Brawn and Robinson 1996).

Most empirical studies documenting sink populations use nesting data and mortality data from the subpopulation, and model population persistence over time in the absence of immigration or emigration (Ricklefs 1973, King and Mewaldt 1987, Stacey and Taper 1992, Pulliam and Danielson 1991, Donovan et al. 1995b). Without immigration, sink populations decline over time and go extinct. With immigration, however, sinks can persist with no detectable declines in numbers over time (Pulliam 1988).

What evidence is there, then, that birds are structured as sources and sinks, and that source-sink status is related to level of landscape-scale fragmentation? The evidence is very weak at this time, in part because we do not yet know the geographic scale that encompasses dispersal movements among sources and sinks. However, there is evidence that reproductive success in fragmented landscapes is too low to compensate for adult mortality (e.g., Donovan et al. 1995b, Trine 1998), and that dispersal occurs among habitat patches. For example, Trelease Woods is an isolated woodlot in central Illinois where bird populations have been censused since 1927 (Kendeigh 1982). In most years, several breeding pairs of Wood Thrush occurred in the woodlot, but three extinction events were recorded that were followed by three colonization events, suggesting that the colonists of unknown origin were not produced locally (Brawn and Robinson 1996).

Although direct evidence to support source-sink structure is weak, predictions generated from population modeling may offer some supporting evidence. Source-sink models suggest that sinks should show relatively higher year to year variation in abundance than source populations (Davis and Howe 1992). As predicted, recent empirical studies demonstrate that populations in fragmented landscapes have greater annual variation than populations in continuous landscapes, which may also affect turnover rates and local extinction (Boulinier et al. 1998). However, it is still unclear whether such variability is due to local processes (such as variability in source-sink status over time), to source-sink dispersal dynamics, or other causes.

THERE IS NO EVIDENCE THAT SINKS OR EDGES FUNCTION AS ECOLOGICAL TRAPS AT A LOCAL SCALE

Although reproductive and survival rates are too low to maintain numbers in sinks, these habitats may benefit the greater source-sink system by "housing" a large number of individuals at any given time. Additionally, a significant number of young may be produced in low-quality habitats, depending on the number of individuals breeding there (Pulliam 1988, Howe et al. 1991).

Is there evidence, however, that maintenance of sink habitat is a detriment to population persistence? Animals often have the opportunity to select among a variety of habitats that vary in quality; preferred habitats are those that are selected disproportionately to other available habitats (Johnson 1980). If individuals avoid low-quality areas, the presence of low-quality habitats may not negatively influence population persistence. However, if individuals select low-quality habitats over available, high-quality habitats for reproduction and survival, then low-quality habitats may function as ecological traps, and their presence may lead to population extirpation (Gates and Gysel 1978, Ratti and Reese 1988, Pulliam and Danielson 1991).

Edges have been suggested to be an ecological trap because they are potentially food rich and have high abundances and diversity of birds, which in turn potentially attract predators searching for food-rich areas (Gates and Gysel 1978, Ratti and Reese 1988). Woodward et al. (2001) examined the ecological trap hypotheses for several species of shrubland-nesting songbirds, and while nesting success varied with distance to edge, they found no evidence that edges acted as ecological traps. Observations of high densities of Wood Thrushes in fragmented Midwest landscapes (Donovan et al. 1995b) have led us to speculate that fragments are similarly acting as traps. High densities of birds in poor-quality fragmented landscapes and low densities in high-quality contiguous landscapes may be the result of: (1) absence of suitable habitat features such as nest sites in contiguous landscapes; (2) displacement of individuals from high quality contiguous landscapes through interspecific competition; or (3) innate preference for habitat characteristics that more commonly occur in fragmented landscapes, such as edge.

Population models suggest that when individuals in the population selected high- and low-quality habitats in proportion to habitat availability in the landscape, landscapes could contain up to 40% low-quality habitat and still promote population persistence. However, when individuals preferred low-quality habitats over high-quality habitats, populations on landscapes containing > 30% low-quality habitat were extirpated, and the low-quality habitat functioned as an ecological trap (Donovan and Thompson 2001). Clearly, much more work is needed to determine the effect of sink habitats on population persistence.

POPULATIONS STRUCTURED AS SOURCES AND SINKS CAN GROW OR DECLINE

Populations structured as sources and sinks can grow or decline depending on the amount of sink habitat, the selection and use of sinks for breeding, and the magnitude of spatial and temporal variation in demographic parameters. It is critical that we examine how our observations of reduced fecundity or density in fragmented landscapes may impact population trends of a source-sink system. We believe our observations of correlations between nesting success and forest cover at the landscape level in the Midwest (e.g., Robinson et al. 1995a) have been uncritically cited as strong evidence that habitat fragmentation causes bird populations to decline. The negative correlation between fragmentation and nesting success offers support for the hypothesis that fragmentation of breeding habitat is causing declines in some songbird population. No one, however, has attempted to evaluate the number of source and sink populations and their effect on a regional population.

For example, Ovenbirds in the Midwest U.S. are thought to be impacted by habitat fragmentation in several ways: they are area-sensitive (Hayden et al. 1985, Burke and Nol 1998), their pairing success on fragments is often significantly lower compared with larger, contiguous patches (Gibbs and Faaborg 1990, Villard et al. 1993), and they have higher daily nest-mortality and parasitism levels in fragments compared with larger patches (Donovan et al. 1995b, Robinson et al. 1995a). Yet, Breeding Bird Survey data suggest that Ovenbirds are maintaining numbers and even increasing in many areas in the Midwest (Sauer et al. 1997). Overall population growth (the growth rate of the entire source-sink system on the landscape) may not be impacted by the poor reproductive success of birds in fragments if breeding individuals generally avoid small patches or if the landscape is dominated by larger patches that are used for breeding.

We have used modeling approaches to test how landscape composition, habitat selection, and nesting success interact to produce population increases or declines at a regional scale (Donovan and Lamberson 2001). The model combined (1) the frequency distribution of patch sizes in the landscape (e.g., highly fragmented landscapes vs. continuously forested landscapes), (2) the distribution of individuals across the range of patches in the landscape (e.g., area sensitive vs. area insensitive vs. edge distribution patterns), and (3) the fecundity of individuals as a function of patch size in the landscape (e.g., fragmentation effects on fecundity vs. no fragmentation effects on fecundity). We used this model to examine population growth under various landscape, distribution, fecundity, and survival scenarios.

Results from the model indicate that the highly cited observation that fecundity decreases as patch size decreases does not necessarily cause landscape level population declines in songbirds. When total habitat in the landscape is held constant, reduced fecundity associated with patch size could lead to population declines when landscapes are highly fragmented, or when landscapes are more continuous, but individuals occur in high densities in small patches and low densities in large patches. Thus, when landscapes offer both large and small patches for breeding (a more contiguous landscape), area-sensitive species can maintain population sizes in spite of decreased fecundity in small patches because birds achieve their highest densities in patches where fecundity is greatest, and high reproduction in such source habitats can maintain sinks within the landscape (Donovan and Lamberson 2001). Two recent large scale analyses of Breeding Bird Survey data have linked population change to fragmentation. Donovan and Flather (2002) found a significant negative correlation between the proportion of a population occupying fragmented habitat and population trend. Boulinier et al. (2001) found that richness of forest area-sensitive species was lower, and year-to-year rates of local extinction higher, on Breeding Bird Survey routes surrounded by landscapes with lower mean forest-patch size.

RESEARCH AND CONSERVATION IMPLICATIONS

We believe there is adequate corroborative evidence for this multi-scale approach to fragmentation to use this as a working model for research and conservation. We believe one of the most important conclusions from our work in eastern forests is that landscape composition is an important determinant of reproductive success, even at a local scale. In eastern forests where concerns are focused on the effects of cowbird parasitism and on generalist predators associated with agricultural and other human-dominated land uses, fragmentation of forests and a reduction in the amount of forest in the landscape results in increased levels of predation and parasitism. Future research should directly test our hypotheses of top-down constraints on reproductive success as well as hypothesized mechanisms for effects at each scale. Research should address the larger scale context of studies and potential differences among predators. There is already evidence that landscape level effects of fragmentation differ between the western and eastern United States (Tewksbury et al. 1998), which is further indication of the importance of top-down constraints and a multi-scale approach.

This model has important conservation implications as well. The importance of large-scale effects suggests that at high levels of fragmentation, conservation efforts should be focused on restoration of the landscape matrix and a reduction in fragmentation. At some level, where the landscape-level effects of fragmentation are no longer critical, local habitat management practices become important. Local management considerations could include management practices to provide appropriate habitat types, minimize edge, or manage habitat structure. Finally, while we believe fragmentation is a major conservation issue in eastern forests, we caution that not all fragmentation needs to be mitigated. Fragmentation of one habitat provides other habitats, and source-sink dynamics suggest that some proportion of a population can reside in sink habitat. A challenge for researchers, land managers, and policy-makers is to determine when fragmentation at a regional or population level is severe enough to drive population declines, and to balance competing species conservation objectives and land use.

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