

# Landscape Level Effects on Forest Bird Populations in Eastern Broadleaf Forests: Principles for Conservation<sup>1</sup>

Frank R. Thompson III<sup>2</sup>

---

## Abstract

Forest fragmentation, urbanization, and forest management are important issues for bird conservation in the eastern broadleaf forest of North America. Fragmentation of forest by agricultural and developed land uses increases the numbers of Brown-headed Cowbirds (*Molothrus ater*) and nest predators in the landscape, which results in decreased productivity of songbirds. Reproductive success is so low in some Midwestern landscapes that the only way populations could persist is through immigration, which provides circumstantial evidence that populations are structured as sources and sinks. Recent hypotheses that put nest-site factors in a habitat context, habitat or local factors in a landscape context, and landscapes in a geographic context provide guidance for conservation planning. At a landscape scale conservation efforts should focus on providing necessary habitats, conserving existing large-contiguous landscapes, and reducing fragmentation in moderately fragmented landscapes. Minimizing habitat fragmentation at a landscape scale may be the best approach to addressing local effects such as edge and patch size effects.

*Key words:* bird conservation, brown-headed cowbirds, eastern broadleaf forest, edge effects, fragmentation, landscapes, nest predators, patch size.

## Introduction

The eastern broadleaf forest in North America ranges from extensively forested to highly fragmented. Important issues for bird conservation in the region are forest fragmentation, urbanization, and forest management. Landscape level patterns and processes, including those above, are key considerations in bird conservation efforts in Eastern forests. Several key studies in the region provide the basis for the fragmentation hypothesis (Donovan et al. 1995, Robinson et al. 1995, Donovan et al. 1997, Thompson et al. 2000; see Thompson et al.

2002 for review). I believe there is sufficient support for the fragmentation hypothesis to consider it a key factor in bird conservation efforts. Fragmentation, however, should be considered along with other factors that occur within a hierarchy of spatial scales that affect bird populations (Thompson et al. 2002).

I review the fragmentation hypothesis, as it pertains to songbird populations, and some of the evidence supporting it. I describe how fragmentation and other processes at larger and smaller scales fit within a spatial hierarchy of factors affecting bird populations, and why this multi-scale model is important to bird conservation in eastern broadleaf forests. While this paper is brief, I refer to key examples, and recent more thorough reviews exist (Faaborg et al. 1995, Walters 1998, Thompson et al. 2002).

## The Fragmentation Hypothesis

The fragmentation hypothesis is that reproductive success of forest songbirds is, on average, lower in fragmented forests than in more contiguous forests. Lower reproductive success is the result of a greater abundance of predators and cowbirds in landscapes fragmented by human-dominated land uses such as agriculture and suburban and urban development. Reproductive success is so low in some landscapes that the only way populations could persist is through immigration, which provides circumstantial evidence that populations are structured as sources and sinks.

Important aspects of the fragmentation hypothesis are that it pertains to landscape-level processes and that it is dependent on fragmentation of forests by habitats with greater numbers of predators and or cowbirds. The interspersing of forest with human-dominated habitats results in a numerical increase in predators and cowbirds at the landscape scale. The hypothesis is independent of smaller scale effects such as edge or patch-size effects. For instance, it does not matter if predation and parasitism are greater in edges or small patches than forest interior, but that, on average, predation and parasitism are greater in fragmented landscapes than non-fragmented landscapes. The converse may not be true, however, because edge or patch size effects may be dependent on levels of fragmentation. This simple distinction, while not immediately intuitive, is important

---

<sup>1</sup>A version of this paper was presented at the **Third International Partners in Flight Conference, March 20-24, 2002, Asilomar Conference Grounds, California.**

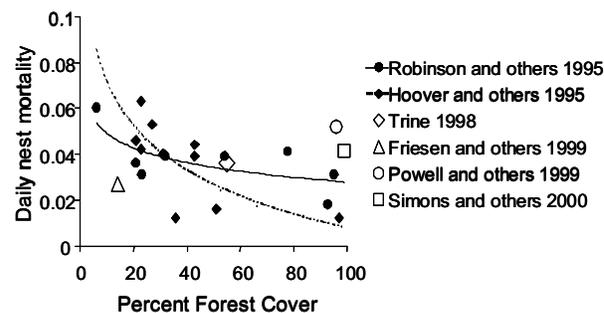
<sup>2</sup>USDA Forest Service North Central Research Station, 202 Natural Resources Bldg., University of Missouri, Columbia, MO 65211-7260. E-mail: frthompson@fs.fed.us.

because it is the increased numbers of predators and cowbirds in the landscape, not their preference (or lack of) for edge, that results in a fragmentation effect. For example, there is stronger support for the effect of landscape level fragmentation effects than either edge or area effects in the abundance of predators (Chalfoun et al. 2002). And, irrespective of their preference for edge, it is the amount of agricultural land (which provides feeding habitat) that appears to regulate cowbird abundance in Midwestern landscapes. For example, some landscapes in Missouri and Illinois that are approximately 50 percent forested vary greatly in mean forest patch size and total amount of edge but all have high cowbird parasitism, whereas those that are greater than 70 percent forested generally have low parasitism (Thompson et al. 2000). I believe a landscape focus, not based on area or edge effects, can provide simple and effective guidance for conservation efforts.

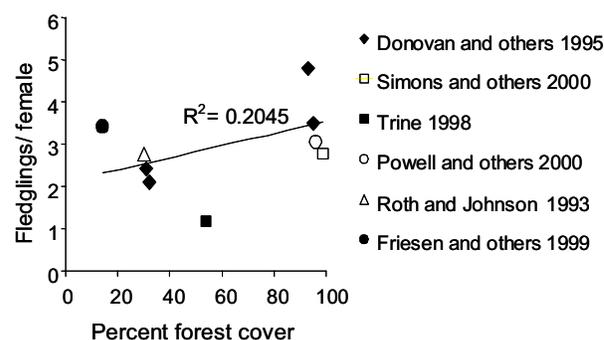
Strong evidence for lesser reproductive success in fragmented landscapes than non-fragmented forests comes from several studies in eastern broadleaf forests (Hoover et al. 1995, Robinson et al. 1995, Donovan et al. 1997). These studies were able to detect a fragmentation effect because they occurred in a context where eastern broadleaf forest was fragmented by agricultural land uses and they examined a wide range of landscape conditions. The fragmentation hypothesis may not apply to western landscapes because of different predator communities, habitat relationships, and a greater level of historical, natural habitat interspersions (Tewksberry et al. 1998). Also, other studies may not have detected these effects because they studied a narrower range of landscape conditions or habitat patches rather than landscapes (i.e. Fauth 2000, Fauth et al. 2000). I compiled data from several eastern studies of nesting success of Wood Thrush (*Hylocichla mustelina*) and plotted them with data from Robinson et al. (1995; *fig. 1*). The additional data points increased variation and do not provide a strong case for or against the patterns reported by Robinson et al. (1995) and Hoover et al. (1995). This could be expected, however, because the additional points represent a broader geographic and temporal span and add additional sources of variation that are not accounted for. Estimates of Wood Thrush productivity in the region, however, do provide general support for lesser productivity in fragmented landscapes (*fig. 2*).

Additional support for fragmentation effects comes from recent studies linking population trends and occupancy to fragmentation. Donovan and Flather (2002) found a significant negative correlation between the proportion of a population occupying fragmented habitat and the population trend. Boulinier et al. (2001) found that species richness of area-sensitive, forest species was lesser, and year-to-year rates of local extinction greater, on Breeding Bird Survey routes

surrounded by landscapes with a small mean forest-patch size.



**Figure 1**— Relationship of Wood Thrush daily nest predation to the amount of forest cover in the landscape based on studies in eastern broadleaf forests. The  $R$ -squares for regression of log-transformed data are 0.54 for Robinson et al. (1995, solid line) and 0.53 for Hoover et al. (1995, dotted line).



**Figure 2**— Relationship of Wood Thrush productivity to the amount of forest cover in the landscape based on studies in eastern broadleaf forests. The  $R$ -square of the regression line is 0.20.

## Population Sources and Sinks

The fragmentation hypothesis implies that nesting success is so low in some landscapes that these populations must be population sinks where population persistence depends on immigration from other populations. Evidence for population sinks is circumstantial and based on very low reproductive success in fragmented habitats (Robinson 1992, Donovan et al. 1995, Robinson et al. 1995) and extirpation and recolonization events (Brawn and Robinson 1996). Reproductive success and source-sink status can vary over time and space. Source populations can have years with low reproductive success (Anders et al. 1997) and some populations in fragmented landscapes can have moderate to high nesting success (Friesen et al. 1999, Fauth et al. 2000).

Nonetheless, the presence of population sinks does not necessarily imply low viability of populations. Donovan

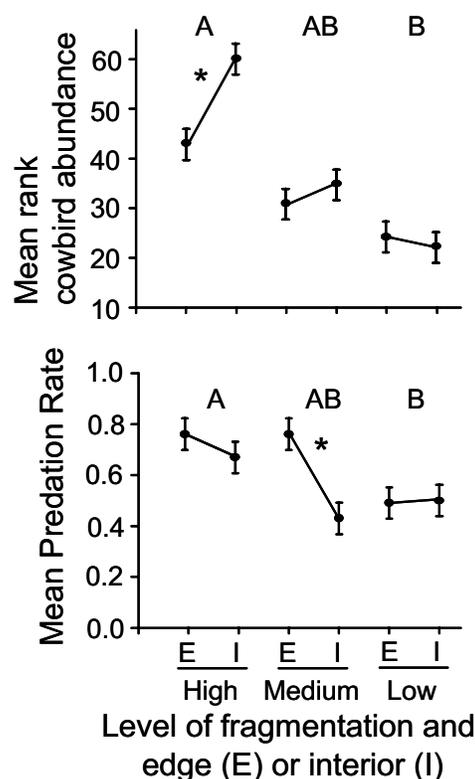
and Thompson (2001) demonstrated that a population could persist even if 40 percent of the habitat is sink habitat. If individuals, however, prefer sink habitat to higher quality source habitat, sinks can function as ecological traps and result in extinction if >30 percent of the habitat is sink habitat. Nevertheless, sink habitat provides habitat within which individuals can reside, and those individuals may have important ecological roles in the community or contribute to the population at a future time.

### Multi-Scale Model of Factors Affecting Populations

Conservation and research will be most effective if it acknowledges that factors affecting breeding birds occur over a range of scales and that larger scales provide context or limit responses at smaller scales. These scales include (1) biogeographic—abundance and distribution of animals (breeding birds, predators, and cowbirds) varies geographically; (2) landscape—this includes fragmentation effects and effects of landscape composition; (3) habitat scale—patch characteristics including habitat type, patch size, and distance to edge; (4) nest patch or site—micro-habitat characteristics directly around the nest or the immediate vicinity of the nest (see Thompson et al. 2000, 2002 for a more thorough review of these factors).

For example, 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 (Donovan et al. 1997). In landscapes with <15 percent forest, predation was high in forest edge and interior; at 45 to 55 percent forest cover, predation was high in forest edge and low in forest interior; and at >90 percent forest cover, predation was low in forest edge and interior (*fig. 3*). Cowbird abundance was much greater in landscapes with high levels of forest fragmentation than those with low levels of fragmentation (*fig. 3*).

The results of this research also were confirmed by a meta-analysis of nest predation 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). Similarly in a meta-analysis of nest predators Chalfoun et al. (2002) determined that predator responses to edges, patch size, and fragmentation were not independent of landscape context. Predator abundance or activity was related to edge, patch area, or fragmentation in 66.7 percent of tests when adjacent land use was agricultural, 5.6 percent when forest, 16.7 percent when grassland, and 5.6 percent when clearcut forest.



**Figure 3**— 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 percent forest; medium, 45-55 percent forest; and low, >90 percent 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).

### Implications for Conservation

I believe the following conservation actions have the greatest potential to benefit breeding birds in eastern broadleaf forests. Planning and management should acknowledge the hierarchical nature of these effects whereby larger scale factors constrain or limit smaller scale effects.

#### Biogeographic

Be aware of geographic patterns in bird, predator and cowbird abundances. Cowbird abundance and parasitism rates generally decrease with distance from the Great Plains (Hoover and Brittingham 1993, Thompson et al. 2000). The abundance of snakes, key songbird predators (Thompson et al. 1999), varies with latitude. As we learn more about how habitat and landscape factors affect individual species of predators, knowledge of the biogeographic context (i.e. predator community) will become more important factors in bird conservation.

## Landscape

### Provide required habitats

Consider the full range of habitats needed by species within the region. Because habitat requirements vary among species some prioritization will have to occur. Mandates for threatened, endangered, sensitive species, and species prioritization schemes can provide guidance. The historic range of variability concept also can provide useful guidance (Committee of Scientists 1999).

### Reduce fragmentation effects

A priority is to conserve large contiguous landscapes because few of these usually exist. The goal is to ensure there are sufficient heavily forested landscapes within the region to meet the needs of forest birds. Research has not identified specific threshold levels for fragmentation effects but some bird conservation planning has targeted landscapes with >70 percent forest cover as priorities for forest bird conservation (Fitzgerald et al. this volume) on the basis of Robinson et al. (1995). Next, consider actions to increase the strength of sources, or convert marginal sinks into sources by converting or managing agricultural habitats to make them less favorable to predators and cowbirds. Efforts to minimize fragmentation should not hinder efforts to restore other important natural communities such as savannas and shrub lands because there is no evidence that these habitats cause the negative, landscape-level effects that human dominated habitat does. Recognize that some proportion of the global population will reside in population sinks, and that sinks can have some value. Therefore, conservation should focus on ensuring that there is adequate source habitat to balance sink habitat, and not necessarily on eliminating sink habitat.

### Habitat interspersions

Habitats can be provided within or among landscapes, depending on desired levels of interspersions and species habitat needs. Consider needs for interspersions and habitats for all life stages including juveniles, non- or post-breeding adults (Anders et al. 1998, Pagen et al. 2000) and migrants.

### Habitat

Addressing landscape level fragmentation is the best approach to reducing patch-size or edge effects. I believe ensuring landscapes are mostly composed of forest will be more effective and efficient in conserving forest birds than focusing on the size and amount of edge in individual patches. Patch size or edge effects are not likely to have negative, population-level effects in minimally fragmented, mostly forested landscapes. In greatly fragmented landscapes edge and area effects may be the result of fragmentation effects, not the cause; remember it is the interspersions of predator and cowbird habitat in landscapes that results in more predators and cowbirds and not edge by itself.

Larger patches and less edge are usually better, assuming you provide desired levels of interspersions within or among landscapes. For example, even though clearcutting may be controversial, it can result in less edge and fragmentation of older forest than selection methods. In addition, it will result in larger patches of early successional forest that are of greater value to many early successional birds than selection methods (Brawn et al. 2001, Thompson and DeGraaf 2001).

While my focus has been on landscape-level management, habitat managers should also consider habitat structure within patches. Eastern forests and habitat needs of songbirds vary greatly in composition and structure. A coarse-grain approach is to ensure native plant communities and disturbance processes occur across large landscapes and assume habitat needs of species will be met. Natural disturbance agents, prescribed fire, and silviculture can be integrated in this approach (Thompson et al. 1995, Brawn et al. 2001). More intensive habitat level management is appropriate where habitat needs are known and there is special interest in target species.

## Acknowledgments

I thank J. Faaborg, T. M. Donovan, S. K. Robinson, and numerous graduate students for their collaboration on many of the ideas and studies reviewed in this manuscript. J. Faaborg and R. Peak provided valuable review of the manuscript.

## Literature Cited

- Anders, A. D., D. C. Dearborn, J. Faaborg, and F. R. Thompson, III. 1997. **Juvenile survival in a population of Neotropical migrant birds.** *Conservation Biology* 11: 698-707.
- Anders, A. D., J. Faaborg, and F. R. Thompson, III. 1998. **Postfledging dispersal, habitat use, and home-range size of juvenile Wood Thrushes.** *Auk* 115: 349-358.
- Bayne, E. M., and K. A. Hobson. 1997. **Comparing the effects of landscape-fragmentation by forestry and agriculture of predation of artificial nests.** *Conservation Biology* 11: 1418-1429.
- Boulinier, T., J. D. Nichols, J. E. Hines, J. R. Sauer, C. H. Flather, and K. H. Pollock. 2001. **Forest fragmentation and bird community dynamics: Inferences at regional scales.** *Ecology* 82: 1159-1169.
- Brawn, J. D., and S. K. Robinson. 1996. **Source-sink population dynamics may complicate the interpretation of long-term census data.** *Ecology* 77: 3-12.
- Brawn, J. D., S.K. Robinson, and F. R. Thompson, III. 2001. **The role of disturbance in the ecology and conservation of birds.** *Annual Reviews: Annual Review of Ecology and Systematics* 32: 251-276.

## Landscape Effects on Bird Populations—Thompson

- Chalfoun, A. D., F. R. Thompson, III, and M. J. Ratnaswamy. 2002. **Nest predators and fragmentation: A review and meta-analysis.** *Conservation Biology* 16: 1-16.
- Committee of Scientists. 1999. **Sustaining the people's lands: recommendations for stewardship of the national forests and grasslands into the next century.** Washington, DC: U.S. Department of Agriculture.
- Donovan, T. M., and C. H. Flather. 2002. **Relationships among North American songbird trends, habitat fragmentation, and landscape occupancy.** *Ecological Applications* 12: 364-374.
- Donovan, T. M., and F. R. Thompson, III. 2001. **Modeling the ecological trap hypothesis: A habitat and demographic sensitivity analysis for migrant songbirds.** *Ecological Applications* 11: 871-882.
- Donovan, T. M., F. R. Thompson, III, J. Faaborg, and J. R. Probst. 1995. **Reproductive success of neotropical migrant birds in habitat sources and sinks.** *Conservation Biology* 9: 1380-1395.
- Donovan, T. M., P. W. Jones, E. M. Annand, and F. R. Thompson, III. 1997. **Variation in local-scale edge effects: Mechanisms and landscape context.** *Ecology* 78: 2064-2075.
- Faaborg, J., M. Brittingham, T. Donovan, and J. Blake. 1995. **Habitat fragmentation in the temperate zone.** In: T. E. Martin and D. M. Finch, editors. *Ecology and management of neotropical migratory birds.* New York, Oxford University Press; 357-380.
- Fauth, P. T. 2000. **Reproductive success of wood thrushes in forest fragments of northern Indiana.** *Auk* 117: 194-204.
- Fauth, P. T., E. J. Gustafson, and K. N. Rabenold. 2000. **Using landscape metrics to model source habitat for neotropical migrants in the Midwestern U.S.** *Landscape Ecology* 15: 621-631.
- Fitzgerald, J. A., C. D. True, D. D. Diamond, T. Ettel, L. Moore, T. A. Nigh, S. Vorisek, and G. Wathen. This volume. **Delineating focus areas for bird conservation in the Central Hardwoods bird conservation region.**
- Friesen, L., M. D. Cadman, and R. J. MacKay. 1999. **Nesting success of Neotropical migrant songbirds in a highly fragmented landscape.** *Conservation Biology* 13: 33-346.
- Hartley, M. J., and M. L. Hunter. 1998. **A meta-analysis of forest cover, edge effects, and artificial nest predation rates.** *Conservation Biology* 12: 465-469.
- Hoover, J. P., and M. C. Brittingham. 1993. **Regional variation in cowbird parasitism of Wood Thrushes.** *Wilson Bulletin* 105: 228-238.
- Hoover, J. P., M. C. Brittingham, and L. J. Goodrich. 1995. **Effects of forest patch size on nesting success of wood thrush.** *Auk* 112: 146-155.
- Pagen, R. W., F. R. Thompson, III, and D. Burhans. 2000. **Breeding and post-breeding habitat use by forest migrant songbirds in the Missouri Ozarks.** *Condor* 102: 738-747.
- Powell, L. A., M. J. Conroy, D. G. Krentz, and J. D. Lang. 1999. **A model to predict breeding-season productivity for multi-brooded songbirds.** *Auk* 116: 1001-1008.
- Powell, L. A., J. D. Lang, M. J. Conroy, and D. G. Krentz. 2000. **Effects of forest management on density, survival, and population growth of Wood Thrushes.** *Journal of Wildlife Management* 64: 11-23.
- Robinson, S. K. 1992. **Population dynamics of breeding neotropical migrants in a fragmented Illinois landscape.** In: J. M. Hagan and D. W. Johnston editors. *Ecology and conservation of Neotropical migrant landbirds.* Washington, DC: Smithsonian Institution Press; 408-418.
- Robinson, S. K., F. R. Thompson, III, T. M. Donovan, D. R. Whitehead, and J. Faaborg. 1995. **Regional forest fragmentation and the nesting success of migratory birds.** *Science* 267: 1987-1990.
- Roth, R. R., and R. K. Johnson. 1993. **Long-term dynamics of a wood thrush population breeding in a forest fragment.** *Auk* 110: 37-48.
- Simons, T. R., G. L. Farnsworth, and S. A. Shriner. 2000. **Evaluating Great Smoky Mountains National Park as a population source for the wood thrush.** *Conservation Biology* 14: 1133-1144.
- Tewksbury, J. J., S. J. Hejl, and T. E. Martin. 1998. **Breeding productivity does not decline with increasing fragmentation in a western landscape.** *Ecology* 79: 2890-2903.
- Thompson, F. R., III, and R. M. DeGraaf. 2001. **Conservation approaches for woody, early successional communities in the eastern United States.** *Wildlife Society Bulletin* 29: 483-494.
- Thompson, F. R., III, W. Dijak, and D. E. Burhans. 1999. **Video identification of predators at songbird nests in old fields.** *Auk* 116: 259-264.
- Thompson, F. R., III, T. M. Donovan, R. M. DeGraaf, J. Faaborg, and S. K. Robinson. 2002. **A multi-scale perspective of the effects of forest fragmentation on birds in eastern forests.** *Studies in Avian Biology* 24: 8-19.
- Thompson, F. R., III, J. R. Probst, and M. G. Raphael. 1995. **Impacts of silviculture: Overview and management recommendations.** In: T. E. Martin and D. M. Finch, editors. *Ecology and management of neotropical migratory birds.* New York, NY: Oxford University Press; 201-219.
- Thompson, F. R., III, S. K. Robinson, T. M. Donovan, J. Faaborg, and D. R. Whitehead. 2000. **Biogeographic, landscape, and local factors affecting cowbird abundance and host parasitism levels.** In: J. N. M. Smith, T. L. Cook, S. I. Rothstein, S. K. Robinson, and S. G. Sealy, editors. *The ecology and management of cowbirds.* Austin, TX: University of Texas Press; 271-279.
- Trine, C. L. 1998. **Wood Thrush population sinks and implications for the scale of regional conservation strategies.** *Conservation Biology* 12: 576-585.

## Landscape Effects on Bird Populations –Thompson

Walters, J. R. 1998. **The ecological basis of avian sensitivity to habitat fragmentation.** In: J. M. Marzluff and R. Sallabanks, editors. Avian conservation research and management. Washington DC: Island Press; 181-192.