

Regional Forest Fragmentation and the Nesting Success of Migratory Birds

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Forest fragmentation, the disruption in the continuity of forest habitat, is hypothesized to be a major cause of population decline for some species of forest birds because fragmentation reduces nesting (reproductive) success. Nest predation and parasitism by cowbirds increased with forest fragmentation in nine midwestern (United States) landscapes that varied from 6 to 95 percent forest cover within a 10-kilometer radius of the study areas. Observed reproductive rates were low enough for some species in the most fragmented landscapes to suggest that their populations are sinks that depend for perpetuation on immigration from reproductive source populations in landscapes with more extensive forest cover. Conservation strategies should consider preservation and restoration of large, unfragmented "core" areas in each region.

The conservation of neotropical migrant bird species, which breed in North America and winter in the tropics, has attracted attention even though most are not yet endangered (1, 2). Many neotropical migrants, however, are suffering population declines, the causes for which may include the loss of breeding, wintering, and migra-

tion stopover habitats (3). A frequently hypothesized cause for declines in populations of migrant birds is the negative impact of habitat fragmentation (4) on breeding success (5). Habitat fragmentation may allow higher rates of brood parasitism by brown-headed cowbirds (*Molothrus ater*) and nest predation (6, 7). Cowbirds lay their eggs in the nests of other "host" species, which then raise cowbirds at the expense of their own young (8).

Populations of cowbirds and many nest predators are higher in fragmented landscapes where there is a mixture of feeding habitats (agricultural and suburban) and breeding habitats (forests and grasslands) (8-10). In landscapes fragmented by agri-

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cultural fields, levels of nest predation and brood parasitism are so high that many populations of forest birds in the fragmented landscapes are likely to be population "sinks" (11) in which local reproduction is insufficient to compensate for adult mortality (12). As landscapes become increasingly fragmented, this reproductive dysfunction could cause regional declines of migrant populations (7).

Previous studies of the effects of fragmentation have focused primarily on reproductive success as a function of local factors such as habitat size or distance to the habitat edge (5, 13). Many studies used artificial nests (14), which may not reflect natural predation levels (15), or relied on composite data from natural nests of many host species (6, 7, 16, 17).

We tested the hypothesis that the reproductive success of nine species of forest birds was related to regional (midwestern United States) patterns of forest fragmentation. We measured nest predation and brood parasitism in nine different landscapes ranging from over 90% agricultural to more than 90% forested. The study areas were in Illinois, Indiana, Minnesota, Missouri, and Wisconsin.

This study involved the coordinated efforts of five teams of 5 to 25 researchers (totaling over 100 assistants) who located and monitored the fates of more than 5000 nests on nine study areas from 1989 to 1993. The study areas represented the entire range of forest fragmentation available in the Midwest (Fig. 1). Each study area consisted of two to nine sites on which nests were monitored every 2 to 7 days to determine if they were parasitized and to calculate the daily predation rate with the Mayfield index (18). Data were pooled from nests in all years and on all sites within a study area (19). Comparing parasitism and predation levels from different years could result in errors, but these should be minimal

because most of the study area estimates are means from several years with an overlap in years among study areas. We include data from nine species for which we have data from at least four sites (20). All species except the northern cardinal are neotropical migrants.

We constructed a map of forest cover for the entire region from 1:250,000 scale digital land use and land cover data derived from thematic overlays (21). A spatial analysis program (FRAGSTATS) (22) was used to calculate the mean percent forest cover, mean percent forest interior (forest >250 m from an edge), and mean forest patch size within a 10-km radius of the center of each site. We then calculated means for the forest statistics from all of the sites within a study area (Fig. 2). For each species, we calculated Pearson correlation coefficients for the relation of the daily nest mortality and percent nests parasitized with the percent forest cover, percent forest interior, and mean forest patch size. We tested the hypothesis that brood parasitism and nest predation were related to the forest cover statistics for all species by combining the probabilities from the species-specific correlations (23). The forest cover statistics were log-transformed when necessary. Percent forest cover, percent forest interior, and mean forest patch size were all highly correlated [all correlations were significant at the 0.001 level, correlation coefficient (r) = 0.89 to 0.985]. We only present results for percent forest cover because it had the highest correlations with nesting success for most species.

Cowbird parasitism was negatively correlated with percent forest cover for all species; correlations were significant [probability (P) \leq 0.05] for five of the nine species studied (Fig. 3). The combined probabilities test (23) indicated that, overall, nest parasitism was significantly negatively related to the amount of forest cover

in the landscape ($P \leq$ 0.01). Most wood thrush nests in landscapes with less than 55% forest cover were parasitized. In some landscapes, there were more cowbird eggs than wood thrush eggs per nest (11). In contrast, cowbird parasitism levels were so low in the heavily forested landscapes that cowbird parasitism is unlikely to be a significant cause of reproductive failure (24).

There were some exceptions to the trends. Parasitism levels were consistently higher in the four Illinois sites than in comparably fragmented forests in the other states. Cowbird abundance was also higher in the Illinois landscapes (10). Several migrant species were heavily parasitized in the mostly forested Indiana landscape where most other species were rarely parasitized. These results suggest that local factors such as the spatial distribution and kinds of forest edges, the quality of cowbird feeding areas, and preferences by cowbirds for particular hosts also influence parasitism.

Levels of nest predation also declined with increasing forest cover for all species. Although only three of the nine species had a significant ($P \leq$ 0.05) negative correlation with percent forest cover (Fig. 4), the combined probabilities test for the overall effect across all species was significant ($P <$ 0.02). Three ground-nesting warblers (the ovenbird and the worm-eating and Kentucky warblers) and two species that nest near the ground in shrubs (hooded warbler and indigo bunting) all had extremely high (6% or higher) daily predation rates in the most

Fig. 1. Distribution of forest habitat in the midwestern United States and locations of the study areas. Abbreviations: CAIL, Cache River, Illinois; CNIL, central Illinois; NCMO, north-central Missouri; NWIL, north-western Illinois; NWWI, north-western Wisconsin; SCMO, south-central Missouri; SOIN, southern Indiana; SWIL, south-western Illinois; and WCWI, west-central Wisconsin.

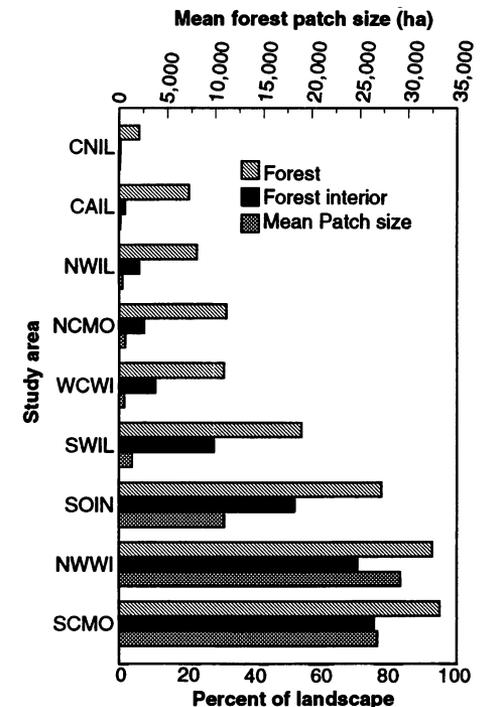
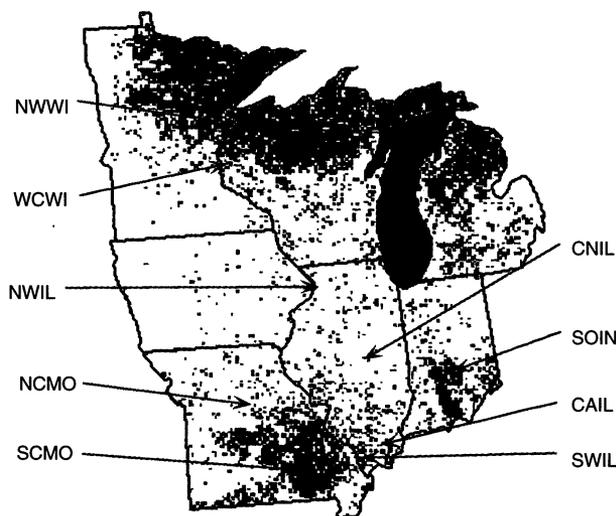


Fig. 2. Forest cover statistics for the nine study areas (landscapes) shown in Fig. 1 in the midwestern United States. Abbreviations as in Fig. 1.

fragmented landscapes. Twelve of the 13 cases of daily predation rates exceeding 7% (>80% of all nests lost to predators) were in the four most fragmented landscapes.

Fragmentation at the landscape scale thus affects the levels of parasitism and predation on most migrant forest species in the midwestern United States. Even the indigo bunting, which prefers forest edges (5), nests more successfully in less fragmented landscapes. Cowbirds can commute up to 7 km between breeding and feeding areas and therefore use widely scattered feeding areas (25). The scale (10-km radius around each study area) on which we measured forest fragmentation is appropriate because it is similar in size to the home ranges of cowbirds. In heavily forested landscapes, cowbird populations may be more limited by the availability of foraging areas than by host availability. In more fragmented landscapes, on the other hand, the cowbird populations may be more limited by the

availability of hosts and may saturate the available breeding habitat, which would result in high levels of parasitism even in the interior (>600 m from the forest edges) of the largest (up to 2200 ha) tracts in Illinois (10). Therefore, landscape-level factors such as percent forest cover determine the magnitude of local factors such as tract size and distance from the forest edges, a result consistent with continental analyses of parasitism levels (25).

Nest predators such as mammals, snakes, and blue jays (*Cyanocitta cristata*) likely have smaller home ranges than cowbirds (26) and may therefore be more affected by local than by landscape-level habitat conditions. Small woodlots in agricultural landscapes, for example, have high populations of raccoons (*Procyon lotor*) (27). Censuses in both Missouri and Wisconsin have shown blue jay and crow (*Corvus brachyrhynchos*) abundances to be much higher in fragmented regions (28). High predation rates of ground- and near-ground-nesting birds in the most fragmented landscapes may reflect the abundance of these predators (29). We know very little, however,

about how fragmentation affects populations of most nest predators.

The large differences between the levels of parasitism and predation in fragmented and unfragmented landscapes (Figs. 3 and 4) provide strong evidence that "source-sink" population models (12) may be applicable. Parasitism levels of wood thrushes, tanagers, and hooded warblers and predation rates on ovenbirds and Kentucky warblers were so high in the most fragmented forests that they are likely population sinks (28). Extensive forests of the Missouri Ozarks, northern Wisconsin, and south-central Indiana have low levels of nest predation and parasitism and may provide the surplus of colonists necessary to maintain populations in fragmented forests in southern Wisconsin, Illinois, and northern Missouri (30). Understanding source-sink population dynamics, however, requires data on the season-long productivity of females and dispersal distances and a better understanding of adult and juvenile mortality (24). Nevertheless, the persistence of migratory songbirds in areas of very low nesting success provides strong evidence for source-sink metapopulation structure (11).

Our results suggest that a good regional conservation strategy for migrant songbirds in the Midwest is to identify, maintain, and restore the large tracts that are most likely to be population sources. Further loss or fragmentation of habitats could lead to a collapse of regional populations of some forest birds (7, 30). Land managers should seek to minimize cowbird foraging opportunities within large, unfragmented sites (8, 10). In more fragmented landscapes, the reduction of cowbird parasitism may require trapping and large-scale restoration efforts (8), whereas reduction of local forest edges may reduce nest predation (14) and increase mating success (29, 31). As long as an adequate number of large, unfragmented regions remain in North America, it is unlikely that fragmentation alone will drive populations of migrant birds to extinction. Increasing fragmentation of landscapes, however, could be contributing to the widespread population declines of several species.

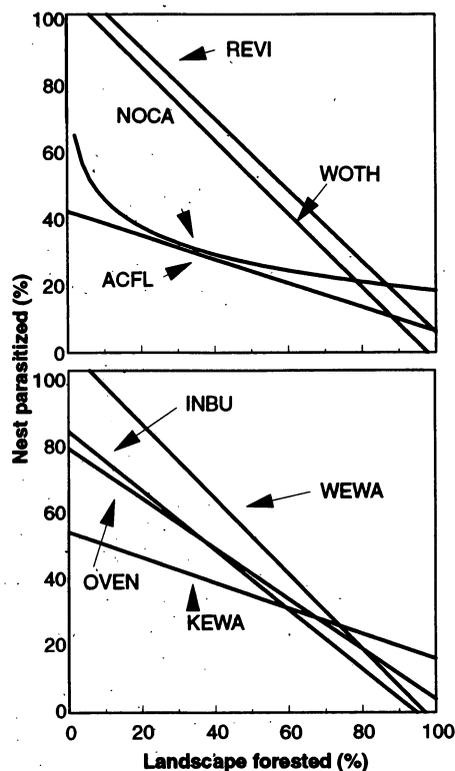


Fig. 3. Correlations between proportion of parasitized nests and percent forest cover in nine study areas (landscapes) in the midwestern United States. Abbreviations: ACFL, acadian flycatcher; INBU, indigo bunting; KEWA, Kentucky warbler; NOCA, northern cardinal; OVEN, ovenbird; REVI, red-eyed vireo; WEWA, worm-eating warbler; and WOTH, wood thrush. For species names, see (20). The statistics for each species are as follows: ACFL ($r = -0.66$, $P = 0.10$), INBU ($r = -0.97$, $P = 0.01$), KEWA ($r = -0.62$, $P = 0.19$), NOCA ($r = -0.69$, $P = 0.12$), OVEN ($r = -0.76$, $P = 0.05$), REVI ($r = -0.94$, $P < 0.01$), WEWA ($r = -0.97$, $P = 0.02$), and WOTH ($r = -0.92$, $P < 0.01$).

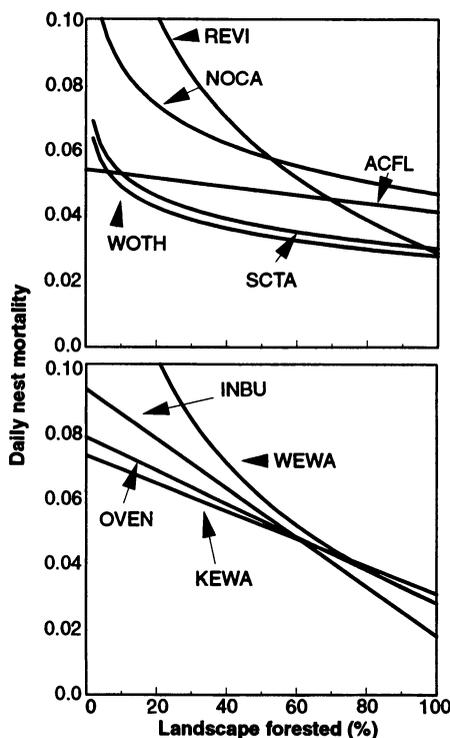


Fig. 4. Correlations between daily nest predation rate and percent forest cover in nine study areas (landscapes) in the midwestern United States. SCTA, scarlet tanager. Other abbreviations are as in Fig. 3. The statistics for each species are as follows: ACFL ($r = -0.12$, $P = 0.79$), INBU ($r = -0.82$, $P = 0.05$), KEWA ($r = -0.67$, $P = 0.14$), NOCA ($r = -0.47$, $P = 0.28$), OVEN ($r = -0.49$, $P = 0.21$), REVI ($r = -0.55$, $P = 0.19$), SCTA ($r = -0.49$, $P = 0.25$), WEWA ($r = -0.99$, $P = 0.01$), and WOTH ($r = -0.74$, $P = 0.02$).

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 19. Study areas included northwestern Illinois (NWIL), five woodlots (90 to 525 ha) (1992–1993 only) in Jo Daviess and Carroll counties; central Illinois (CNIL), three woodlots (65 to 300 ha) in Shelby, Champaign, and Piatt counties; southwestern Illinois (SWIL), four areas in 1000- to 3500-ha tracts in the Shawnee National Forest and Trail of Tears State Forest in Union and Alexander counties; Cache River, IL (CAIL), six study sites in 25- to 1600-ha forests in the Cache River Bioreserve of Johnson, Union, Pulaski, and Alexander counties; southern Indiana (SOIN), four study sites (ranging from 133 to 190 ha) in a >40,000-ha forest tract in the vicinity of the Pleasant Run Unit of Hoosier National Forest of Monroe, Brown, Jackson, and Lawrence counties; northwestern Wisconsin (NWWI), six study areas within the Chequamegon National Forest, Bayfield County; west-central Wisconsin (WCWI), six study areas (80- to 160-ha patch size) along the St. Croix River in Washington and Chisago counties, MN, and Polk County, WI; south-central Missouri (SCMO), eight study areas within the contiguous Ozark Forests in Shannon, Reynolds, and Carter counties; north-central Missouri (NCMO), nine study sites within Boone, Callaway, and Randolph counties in tracts ranging from 150 to 900 ha.
 20. Study species included the acadian flycatcher (ACFL) *Empidonax virescens*, wood thrush (WOTH) *Hylocichla mustelina*, red-eyed vireo (REVI) *Vireo olivaceus*, ovenbird (OVEN) *Seiurus aurocapillus*, worm-eating warbler (WEWA) *Helminthos vermivorus*, Kentucky warbler (KEWA) *Oporornis formosus*, scarlet tanager (SCTA) *Piranga olivacea*, northern cardinal (NOCA) *Cardinalis cardinalis*, and indigo bunting (INBU) *Passerina cyanea*. Sample sizes per species ranged from 50 nests (SCTA) to over 500 (ACFL and WOTH).
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 30. For source-sink models of the wood thrush and ovenbird in this landscape, see T. M. Donovan, R. H. Lamberson, F. M. Thompson III, J. Faaborg, *Conserv. Biol.*, in press; T. M. Donovan, F. R. Thompson III, J. Faaborg, J. Probst, *ibid.*, in press.
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