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THE DEMOGRAPHY OF NEOTROPICAL MIGRANT BIRDS IN HABITAT SOURCES AND SINKS

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and hereby certify that in their opinion it is worthy of acceptance.

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ABSTRACT

Many animal populations exist as geographically isolated subpopulations that are linked by dispersal. Understanding the conditions in which subpopulations persist or go extinct and the factors that influence dispersal among subpopulations is a central problem m ecology and' conservation biology. I used a comparative approach to determine how habitat size and shape affects the demography of three forest-nesting migrants in two regions in the United States. In both regions, I studied the distribution and reproductive success of Ovenbirds (Seiurus aurocapillus), Red-eyed Vireos (Vireo olivaceus), and Wood Thrushes (Hylocichla mustelina). in fragmented and contiguous habitats. In both regions, distribution of individuals was not negatively altered by fragmentation, but total nest failure was significantly higher on fragments than contiguous forests. This increase in total nest failure and a reduction in the number of host fledglings on fragments was attributed to increased nest predation and increased brood parasitism by the Brown-headed Cowbird. The reproductive success of populations of the forest-nesting passerines studied was directly related to spatial pattern of their breeding habitat. Populations in fragmented landscapes functioned as sinks and populations on contiguous landscapes functioned as sources.

I used simple population growth models to estimate viability in the absence of immigration among subpopulations, and modeled how fragmentation of contiguous habitat influenced population size and structure when individuals could disperse among subpopulations. Model results indicate that the reduction in density or extinction of some bird species on small habitats may be the result of two non-exclusive processes: 1) poor reproductive success in small habitats when immigration is negligible, or 2) fragmentation of contiguous habitat, which affects the number of immigrants available to "rescue" populations on fragments from extinction. Because migratory passerines are vagile organisms and dispersal among subpopulations is likely, I emphasize the need to identify

and protect large, intact source habitats throughout a species' breeding range until the spatial scale at which subpopulations interact can be determined.

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CHAPTER I

ECOLOGICAL TRADE-OFFS AND THE INFLUENCE OF SCALE ON BROWN-HEADED COWBIRD DISTRIBUTION

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ABSTRACT

The distribution of Brown-headed Cowbirds (Molothrus ater) should reflect the distribution of their feeding (agricultural or grassy areas) and breeding (host) resources. Because an increase in one resource (e.g. agricultural areas) is often at the expense of the second resource (forest hosts), the relationship between cowbird abundance, forest area, and number of hosts should reflect this apparent trade-off. We studied cowbird distribution and abundance in the extensively forested Missouri Ozarks and in fragmented central Missouri. Cowbirds were more abundant on fragments than on fragmented Ozark study areas ($P = 0.0001$), even though hosts were more abundant in the Ozarks ($P = 0.0042$). In the Ozarks, there was no relationship between cowbird and host abundance, presumably because cowbirds were limited by feeding resources there. By contrast, cowbirds abundance on fragments was positively related to host abundance ($P = 0.0074$), presumably because food was not limited there. Although cowbirds frequently occur in fragmented landscapes, their reproductive success ultimately depends upon the ability of their hosts to successfully fledge them. We examined the nesting success of cowbirds in habitats of varying sizes and shapes. The number of cowbird eggs per nest increased as forest size decreased ($P = 0.0001$), but daily survival of cowbirds in the nest tended to increase as forest size increased ($P = 0.0001$). Thus, a second type of trade-off occurred between clutch size and fledging success such that fledging success was low where many eggs were laid, and fledging success was high where fewer eggs were laid.

We examined habitat characteristics at varying spatial scales (1, 3, 5, and 10 km radius circles) to determine what habitat scale best explains cowbird distribution and abundance. Abundance was strongly related to percent forest cover and forest perimeter to area ratio at the 3-5 km radius scale ($P < 0.001$ for all analyses). These results suggest that Brown-headed Cowbirds are regulated by habitat characteristics at larger spatial scales than the traditionally viewed local scale, and that future cowbird population control depends upon land-management at larger scales.

INTRODUCTION

A species' distribution and abundance is often a function of the distribution of its resources (Brown 1984). For Brown-headed Cowbirds (Molothrus ater), food resources are distributed in open grassy or agricultural areas whereas breeding resources (hosts) are I often distributed in forested areas (Rothstein et al. 1984, Thompson in press). The probability that a cowbird occurs in a forest therefore depends upon the probability that a feeding area is nearby. As areas become more forested, cowbird breeding opportunities may increase but feeding opportunities may decline. Conversely, as forest habitat is converted to agricultural habitat, feeding opportunities may increase but breeding opportunities may decrease because cowbirds parasitize grassland hosts less frequently than forest hosts (Pent and Petit, in press). The occurrence of cowbirds within landscapes that vary in the amount of forest and feeding areas should reflect this apparent trade-off between breeding and feeding resources.

A second type of trade-off is also expected to occur within landscapes of varying forest cover. Cowbird production ultimately depends upon the nesting success of host species (Lowther 1993). Cowbird hosts on small, fragmented forests often experience higher nest predation than hosts on large, unfragmented forests (Wilcove 1985, Askins et al. 1990 and references therein, Robinson et al. 1992). In fragmented landscapes, the distribution of breeding and feeding resources may be optimal for cowbirds. Such landscapes provide food resources necessary for cowbird egg production, but also provide suitable habitat for many nest predators. Thus, cowbirds that lay their eggs in nests within a highly fragmented landscape may experience low nesting success because host nests are frequently depredated. Such fragments may constitute cowbird "population sinks", where reproduction does not compensate for adult mortality (Pulliam 1988). By contrast, cowbirds in large unfragmented forests may be food limited, but predation in large forest tracts is low, and cowbirds that lay eggs there may be more successful than their counterpart's in fragmented forests.

Our goal was to document cowbird distribution in landscapes that vary in the amount of forest to non-forest cover and to examine cowbird reproductive success in such landscapes. Our objectives were to: 1) compare cowbird abundance between fragmented central Missouri forests and the extensively forested Ozark region, 2) determine if cowbird abundance is related to the number of hosts (breeding resources) in fragmented and unfragmented habitats, 3) compare the nesting success of cowbirds in forests of varying size, and 4) examine the relationship between cowbird abundance and the distribution of forested (breeding) and non-forested (feeding) areas at several landscape scales.

METHODS

Cowbird Distribution and Abundance

We studied Brown-headed Cowbird distribution and parasitism on 17 study plots within 7 forest tracts of varying size and shape in Missouri from 1991-1993 (Table 1). A total of 9 fragmented study plots were situated in the highly fragmented central Missouri landscape, and 8 total study plots were situated within the heavily forested Ozarks in southeast Missouri (Figure 1). In 1991, 9 fragmented plots and 6 contiguous forest plots were studied. In 1992, two additional plots were added within contiguous forest and one fragmented plot was dropped from the study. Study plots were approximately 22 hectares; forest tracts containing study plots ranged from 7.4 to 18,258 km^2 (Table 1). Plots were located within mature oak-hickory forest and appeared to be homogeneous in forest structure (Weeny et al. 1993). The non-forested portion of these landscapes was predominantly cool-season pasture.

We gridded each study plot in 150 m intervals. Grids were established by randomly selecting a point within the forest and situating a grid around that point. Fifteen points along grid intersections were designated as "counting points". All counting points were located > 70 meters from an ecotonal edge between forest and non-forest habitat.

Within each plot, we surveyed abundance of Brown-headed Cowbirds and potential hosts by 10 minute point counts (Verner 1988) at the 15 counting points. Each point was

Counted 4 times during the breeding season. Three to 4 different observers conducted counts each year to minimize observer variability (Verner 1989). Counts began after most territories were established (>May 5) and ended by mid-June when most nests had fledged young.

In each 10 minute count, bird detections were recorded within 50- and 70-m fixed radius circles, as well as total (unlimited distance) detections. The mean number of detections in each distance class was computed for each plot in each year. Mean detections at a plot were based on 15 counting points that were censused 4 times within a season (n = 60 counts). We selected the appropriate distance class for analysis based on univariate F-tests. The unlimited distance class was used in all analyses because it yielded the highest F-value in discriminating Brown-headed Cowbirds on fragments and contiguous forests (Bradley and Schumann 1957).

Female cowbirds were differentiated from males based on ‘rattle’ or ‘chatter’ calls (Darley 1968). Because female cowbirds are responsible for parasitism and its consequences for host species, we present point count results for female cowbird detections alone and for all cowbird (male and female) detections. Caution must be used in interpreting female detections based solely on rattle calls because the social context in which these calls are given and how they influence detectability are poorly understood (Lowther 1993).

We compared cowbird abundance on fragmented (n=9 plots) and contiguous forests (n = 8 plots) using a repeated measures analysis of variance, with landscape (fragmented or contiguous) as a main effect and year as a repeated effect. Replicate plots within a landscape were used as the error term.

Relationship of Host Abundance and Cowbird Abundance

Host abundance was surveyed in the same manner as Brown-headed Cowbirds, and consisted predominantly of singing males. We identified hosts as those species which breed during the time Brown-headed Cowbirds were censused and which receive Brown headed cowbird eggs in > 10% of their nests (based on nests located within the study plots I and parasitism rates in the literature). For example, we considered rejector species such as American robin (Turdus migratorius) a host because cowbirds lay their eggs in robin nests, but not blue-gray gnatcatchers (Polioptila caerulea) because most gnatcatcher nests fledged before censuses began. We summed the number of potential hosts at a given plot in a year over all host species, and used all observations of hosts to compute mean host abundance for each plot.

We compared host abundance on fragmented (n = 9 plots) and contiguous forests (n = 8 plots) using a repeated measures analysis of variance, with landscape (fragmented or contiguous) as a main effect and year as a repeated effect. Plots within a landscape were used as the error term.

The relationship between cowbird abundance and host abundance at the plot level was determined using an analysis of covariance, with landscape (fragmented or contiguous) as a covariate. We were interested in determining if the relationship between cowbirds and hosts depends upon the landscape in question.

Reproductive Success of Cowbirds in Landscapes of Varying Forest Cover

Nests that contained cowbird eggs were located in 1991-1993 on 4 forest tracts of varying size and were monitored every 3 to 5 days. These forest tracts included the Ashland, Hungry Mother, and Bennitt fragments and the unfragmented Ozarks (Table 1). For each parasitized nest, we recorded the number of cowbird eggs, chicks, and fledglings.

We determined the mean number of cowbirds per nest in each forest, and used Spearman's rank correlation to determine if there was an association between the number of cowbird eggs per nest and log forest area.

We calculated daily survival of cowbirds on a *per egg* basis (hayfield 1975), and used those estimates to determine the probability that a cowbird egg would survive to fledging (= nesting success). Because we were interested in determining cowbird nesting success on forests of varying size, and because hosts were similar among forests of varying size, we combined host species within a site to determine cowbird survival for each forest. We used Spearman's rank correlation to determine if there was an association between cowbird daily nest survival and log forest area.

Landscape Patterns and Cowbird Abundance at Selected Spatial Scales

Because cowbird distribution may represent a trade-off between feeding and breeding resources, it is important to determine the habitat scale that regulates cowbird distribution. We used an existing forest-cover GIS database developed by the Missouri Department of Conservation and the Geographic Resources Center at the University of Missouri-Columbia (Giesmann et al. 1986) to compute landscape statistics at 1, 3, 5, and 10 km radius spatial scales (see below). The distribution of forestland in Missouri was determined by using photographic images from a Landsat Satellite Thematic Mapper. Areas > 5 acres with at least 10% canopy cover were considered forested habitat and were digitized using an Analytical Mapping System. Files were incorporated into a GIS system, and Map Overlay Statistical System (MOSS) was used to manage digitized data to produce forest area estimates and maps.

We located all seventeen study plots within the GIS database. Some fragmented study plots were situated within the same forest polygon; all plots within the heavily forested Ozarks were situated within the same forest polygon (Table 1). For fragments, we averaged cowbird defections among plots that were located within the same forest polygon for analyses (n = 6). Although all 8 contiguous plots were located within the unfragmented Ozarks, these plots were spatially located as 4 paired plots that were separated by > 5km, and thus the four 'pairs' were considered as independent. We averaged cowbird defections of paired plots for analyses (n = 4). For clarity, these 10 forests (n = 6 fragments and 4 contiguous) will be called 'sites ; sites consist of 1 - 2 study plots (Table 1).

We calculated the % forest cover and perimeter to area ratio within 1, 3, 5, and 10 km radius circles of each site (Figure 2 and Table 1). We evaluated the relationship between cowbird abundance at a site (n =10) and percent forest cover and perimeter/area ratios at these scales. This scale of evaluation is appropriate because female cowbirds move up to 10 km between feeding and breeding areas (Thompson in press, Rothstein et al. 1984).

We used simple, univariate regression models to determine if linear relationships exist between cowbird abundance, cowbird survival, and percent forest cover and perimeter to area ratio across sites at the 1-10 km radius scales. We examined the adjusted R2 for each model to determine the scale (1, 3 ,5, or 10 km radius circles) in which the linear relationship is strongest.

RESULTS

Cowbird Distribution and Abundance

Brown-headed Cowbirds occurred more frequently on fragmented central Missouri plots than the extensively forested Ozark plots (Table 2). Results were similar for analyses based solely on female cowbird defections (Table 2). Additionally, cowbirds increased between 1991 and 1992 (repeated measures analysis of variance main effect of year; F = 18.00; P = 0.0011), and this increase was greater on fragments than contiguous forests (landscape x year interaction; F = 15.98; P = 0.0018).

Relationship of Host Abundance and Cowbird Abundance

Although cowbirds were more abundant on fragments, hosts were more abundant in unfragmented habitat (Table 2). The frequency of cowbird occurrence was related to the number of potential hosts at a plot, but this relationship depended on the forest landscape in question (analysis of covariance host*landscape interaction, F = 7.01; P = 0.0134). On fragmented study plots, cowbirds (males and females combined) were positively related to the number of hosts (Figure 3). This trend was not significant when examining female cowbirds alone (F = 2.70; P = 0.121; $R^2 = 0.153$). By contrast, cowbird (males and females combined) and host abundance was not related in unfragmented Ozark plots (F = 3.11; P = 0.1035; $R^2 = 0.21$).

Reproductive Success of Cowbirds in Landscapes of Varying Forest Cover

We analyzed the incidence of multiple parasitism and nest survival on four forests of varying size. In the Ozarks, parasitism was almost nonexistent; of >500 host nests located in the Ozarks, only 11 nests were parasitized (Faaborg and Clawson, unpublished data). On the 3 fragments, 44 nests containing 123 cowbird eggs or young were located. Nests in the Ozarks were, without exception, singly parasitized, whereas nests on fragments were multiply parasitized (mean = 2.55, standard deviation = 1.35, t = 7.56, P = 0.0001). The number of cowbird eggs per nest increased as forest size decreased (Spearman's Rank Correlation r = -1.00, P = 0.0001, Figure 4). By contrast, cowbird nesting success (the probability a cowbird egg would survive to fledging) increased as forest size increased (Spearman's Rank Correlation r = 1.00, P = 0.0001, Figure 4).

Landscape Patterns and Cowbird Abundance at Selected Spatial Scales

Cowbird abundance (male and female) was not related to forest area at the 1 km scale ($P = 0.073$), but was negatively related to forest area at the 3, 5, and 10 km scales ($P = 0.0023$, 0.0005, and 0.0001, respectively, Table 3). The variation in cowbird abundance was best explained by the variation in percent forest cover at the 10 km scale (adj. $R^2 = 0.854$; Table 3). The abundance of female cowbirds was negatively related to percent forest cover at all spatial scales analyzed (Table 3). The variation in female cowbirds was best explained by variation in percent forest cover at the 3 km - 5 km scale (adj. $R^2 = 0.93$ for both scales; Table 3).

Cowbird abundance was also related to the perimeter to area ratio of the landscape in question. The variation in cowbird abundance was positively related to the variation in perimeter:area ratio at the 3, 5, and 10 km scales ($P = 0.0087$, 0.0019, and 0.0005, respectively), but not the 1 km scale ($P = 0.11$, Table 3). Female cowbirds showed a similar pattern but were significantly related to perimeter:area ratios at all scales examined (Table 3). As with forest area, the relationship between cowbird abundance and habitat edge was best explained at spatial scales > 3 km (Table 3).

Host abundance was positively related to percent forest cover and negatively related to perimeter to area ratio at the 3, 5, and 10 km scales ($P = 0.041$, 0.034, 0.042 and $P = 0.033$, 0.026, 0.0365 respectively, Table 3). Host abundance was not related to percent cover or perimeter to area ratio at the 1 km scale ($P = 0.077$ and 0.177 respectively).

DISCUSSION

Cowbird Distribution and Abundance

Cowbirds evolved in open grasslands where their breeding and feeding resources overlapped spatially (Lowther 1993). Pre-settlement cowbird populations were potentially limited because many sympatric hosts evolved strategies against parasitism (Briskie et al. 1992). In the past 200 years, however, cowbirds have benefited tremendously by the clearing of forests for agricultural purposes, and their populations have exploded (Brittingham and Temple 1983). These changes in landscape have increased feeding resources (agriculture) and introduced new breeding resources (naive hosts) that were previously inaccessible to cowbirds.

Telemetry studies in Missouri and New York show that although feeding and breeding resources can overlap spatially, cowbirds move eat distances between them to optimize the utilization of each resource (Thompson, in press, Hahn, in press). In Missouri, female cowbirds tend to breed in host-rich forests in the early morning and move to open grassy or agricultural areas to feed as the day progresses (Thompson, in press). Our results show that cowbirds occur more frequently on central Missouri fragments than in the unfragmented Ozarks. In the Ozarks, feeding areas are limited and there may be a greater energy cost of moving longer distances to abundant host resources. By contrast, central Missouri forest-agricultural landscapes possess both breeding and feeding resources for cowbirds whose distributions are enhanced with fragmentation.

Beyond a point, however, severely fragmented landscapes may also limit cowbirds by limiting host resources. Again, there may be an energetic cost of traveling between breeding and feeding areas in such landscapes. The smallest fragment we studied was 70 ha in size, perhaps too large for hosts to be limited. We suggest that future studies focus on determining the distribution of cowbirds across an even broader spectrum of forest/field landscapes.

Trade-offs in Host Abundance, Cowbird Abundance, and Reproductive Success

Although cowbirds breed in a wide variety of habitats, several studies suggest that cowbirds select habitats with high host densities (Rothstein et al. 1986, Verner and Ritter 1983, Thompson et al. in press, but see Holford and Roby in press). However, this relationship may depend upon whether feeding resources are nearby. Cowbird abundance was not related to host abundance in large unfragmented forests, despite an abundance of breeding opportunities, presumably because cowbirds were limited by feeding resources.

In fragmented landscapes, cowbird occurrence at a site was positively related to the number of hosts at that site. Two hypotheses might explain this relationship. First, cowbirds may actually assess the number of potential hosts at a particular site and respond accordingly. Alternatively, cowbird abundance may be. related to host abundance because of philopatry (Payne 1977). If cowbirds successfully fledge in fragmented landscapes, the relationship between cowbirds and hosts could be an artifact of site fidelity to their birthplace.

The total number of forest hosts and host densities decrease as forest area decreases (Askins et al. 1990, Wenny et al. 1993), creating an interplay between forest size, host abundance, and cowbird abundance in fragmented landscapes. As forest size decreased, hosts were less common but cowbirds increased. As forest size increased, hosts abundance increased but cowbirds decreased in number. We found that host nests in fragments were often multiply parasitized and had low nesting success, while host nests in the Ozarks were singly parasitized and had higher nesting success. Thus, there was a trade-off between cowbird occurrence, host occurrence, and cowbird nesting success, and selection may favor cowbirds that lay in larger forests. If more cowbirds are produced in larger forests, and natal site fidelity is high, a positive feedback loop may be set in motion with more cowbirds produced in areas of high host abundance. As yet, there is no direct evidence that this is occurring. A clear understanding of such trade-offs requires studying host and cowbird distribution and cowbird nesting success across many landscapes that vary in their distribution of cowbird breeding and feeding areas.

It would be interesting to compare the lifetime fitness of females that parasitize hosts on fragments with that of females that parasitize hosts on larger forest tracts. Assuming that cowbirds are fairly philopatric, females in fragmented habitats surrounded by open, grassy areas are less likely to be food limited and can allocate their energy towards egg production. Although nesting success in fragmented landscapes is relatively low, cowbird populations there may sustain themselves by laying large numbers of eggs.

By contrast, females in unfragmented habitats may produce fewer eggs because opportunities to feed there are restricted. Holford and Roby (in press) reported that when dietary calcium was limited, female cowbirds reduced their laying rate. In addition, females that travel to large forests to lay eggs could experience a higher energetic cost of travel and may arrive to the nest site later than females that lay eggs in fragmented habitat (e.g., Burhans in press). Despite the reduced feeding opportunities and egg laying rates, females in contiguous forests may achieve the same level of fitness as females on fragmented landscapes if hosts escape the high rates of nest predation found in fragmented landscapes.

Cowbird Abundance and Habitat Features at Selected Spatial Scales

Our analyses suggest that cowbird occurrence is best explained by forest cover and perimeter to area ratio at larger spatial scales. Most distributional studies have focused on local-scale processes, and showed significant relationships between cowbird abundance and habitat size and shape (Robinson et al. 1993). Our results concur and showed that female cowbirds were significantly related to forest area and perimeter to area at the 1 km scale. However, this relationship was not detected when considering male and female cowbirds together. These results suggest that: 1) cowbird distribution is regulated at larger scales (see below), 2) landscape patterns differentially regulate male and female cowbird distributions, or 3) male and female cowbirds respond to local-scale landscape patterns, but this was not detected because of an inherent bias in the way we computed forest area. at small scales. Because the centers of the study sites were always located within a forest, all sites were over 45 % forested at the 1 km scale.

Although local scale habitat characteristics may influence cowbird distribution, we emphasize that cowbird populations may be regulated at larger spatial scales than previously thought For female cowbirds, the cowbird distribution to forest cover relationships were the strongest when habitat characteristics are examined in a radius of 3 5 km from the study site. For all cowbirds, these relationships gained strength as scale increased (Table 3). These results suggest that in managing cowbird numbers, habitat characteristics should be evaluated beyond the local scale (see also Hahn, in press, Yamasaki et al., in press).

There are also strong biological reasons that may underlie the patterns we detected. Telemetry studies of female cowbirds in fragmented central Missouri revealed that cowbirds move on average 1- 2 km between breeding and feeding areas (range 0.03 - 7.34 km; Thompson, in press) and that movement between these areas can be greater than expected (i.e, suitable feeding and breeding habitat is apparently by-passed) to optimize the utilization of these resources. Because cowbirds can move great distances to optimize their resource use, we suggest that managing for forest area or perimeter to area ratios may have little impact on cowbird distribution if the surrounding landscape provides optimal cowbird feeding and breeding resources.

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LITERATURE CITED

Askins, R., J. F. Lynch, and R. Greenberg. 1990. Population declines in migratory birds in eastern North America. Curr. Ornith. 7:1-57.

Bradley, R. A., and D. E. Schumman. 1957. The comparison of the sensitivities of similar experiments: applications. Biometrics 13:496-510.

Briskie, J. V., S. G. Sealy, and K. A. Hobson. 1992. Behavioral defenses against avian brood parasitism in sympatric and allopatric host populations. Evolution 46:334-340.

Brittingham, M. C., and S. A. Temple. 1983. Have cowbirds caused forest songbirds to decline? BioSci. 33:31-35.

Brown, J. H. 1984. On the relationship between abundance and distribution of species. Am. Nat. 124:255-279.

Burhans, D. E. In press. Dawn nest arrivals and aggression in two Cowbird hosts: early bird catches the brood parasite. In The ecology and management of Cowbirds (T. L. Cook, ed.). University of Texas Press, Austin, Texas.

Darley J. A. 1968. The social organization of breeding Brown-headed Cowbirds. Ph.D. Dissertation., Univ. West. Ontario, London.

Giessman, N. F., T. W. Barney, T. L. Haithcoat, J. W. Myers, and R. Massengale. 1986. Distribution of forestland in Missouri. Trans. Missouri Acad. Sci. 20:5-20.

Hahn, D. C. In press. Parasitism at the landscape scale: Do Cowbirds prefer forests? In The ecology and management of Cowbirds (T. L. Cook, ed.). University of Texas Press, Austin, Texas.

Holford, K. C., and D. D. Roby. In press. What limits the fecundity of Brown-headed Cowbirds? In The ecology and management of Cowbirds (T. L. Cook, ed.). University of Texas Press, Austin, Texas.

Lowther, P. 1993. Brown-headed Cowbird (VII hr . In The Birds of North America, No 47 (A. Poole and F. Gill., Eds.). Philadelphia: The Academy of Natural Sciences; Washington D.C.: American Ornithologists Union.

Mayfield, H. F. 1975. Suggestions for calculating nest success. Wilson Bull. 87:456-466.

Payee, R. B. 1977. The ecology of brood parasitism in birds. Ann. Rev. Ecol. Syst. 8:1-28.

Petit, L. J., and D. R, Petit. In press. Host selection by Cowbirds in North America: Adaptation to life history traits or ecological opportunism? In The ecology and management of Cowbirds (T. L. Cook, ed.). University of Texas Press, Austin, Texas.

Pulliam, H. R. 1988. Sources, sinks, and population regulation. Am. Nat. 132:652-661.

Robinson, S. K. 1992. Population dynamics of breeding Neotropical migrants in a fragmented Illinois landscape. Pages 408-418 'fin Ecology and conservation of Neotropical migrant landbirds. (J. H. Hagan, III and D. W. Johnston, Eds.). Smithsonian Institution Press, Washington and London.

Robinson, S. K., J. A. Grzybowski, S. I. Rothstein, M. C. Brittingham, L. J. Petit, and F. R. Thompson. Management implications of Cowbird parasitism for Neotropical migrant songbirds. In press. In Proceedings of a workshop on the status and management of neotropical migratory birds. Rocky Mountain Forest and Range Experiment Station General Technical Report, Fort Collies, CO.

Rothstein, S.I., J. Verner, and E. Stevens. 1984. Radio-tracking confirms a unique diurnal pattern of spatial occurrence in the parasitic Brown-headed Cowbird. Ecology 65:77-88.

Rothstein, S. L, D. A. Yokel, and R. C. Fleischer. 1986. Social dominance, mating and spacing systems, female fecundity, and vocal dialects in captive and free ranging Brown-headed Cowbirds. Curr. Ornithol. 3:127-185.

Thompson, F. R. III. In press. Temporal and spatial patterns of breeding Brown-headed Cowbirds in the midwestern United States. Auk.

Thompson, F. R. III, S. K. Robinson, T. M. Donovan, J. Faaborg, and D. R. Whitehead. In press. Biogeographic, landscape, and local factors affecting Cowbird abundance and host parasitism levels. In The ecology and management of Cowbirds (T. L. Cook, ed.). University of Texas Press, Austin, Texas.

Verner, J. and L. V. Ritter. 1983. Current status of the Brown-headed Cowbird in the Sierra National Forest. Auk 100:355-368.

Verner, J. 1988. Optimizing the duration of point counts for monitoring trends in bird populations. Pacific Southwest Forest and Range Experiment Station, Forest Service, USDA Res. PSW-395:1-4.

Verner, J., and K. A. Milne. 1989. Coping with sources of variability when monitoring population trends. Ann. Zool. Fennici 26:191-199.

Wenny, D. G., R. L. Clawson, J. Faaborg, and S. L. Sheriff. 1993. Population density, habitat selection and minimum area requirements of three forest-interior warblers in central Missouri. Condor 95:968-979.

Wilcove, D. S. 1985. Nest predation in forest tracts and the decline of migratory songbirds. Ecology 66:1211-1214.

Yamasaki, M., T. M. McLellan, R. M. DeGraaf, C. A. Costello, and L. A. Rowse. In press. Effects of land-use and management practices on the presence of Brown headed Cowbirds in the White Mountains of New Hampshire and Maine. In The ecology and management of Cowbirds (T. L. Cook, ed.). University of Texas Press, Austin, Texas.

Figure 1. Forest cover (shaded) of Missouri showing general locations of study sites within fragmented central Missouri and unfragmented Ozarks in southeast Missouri.

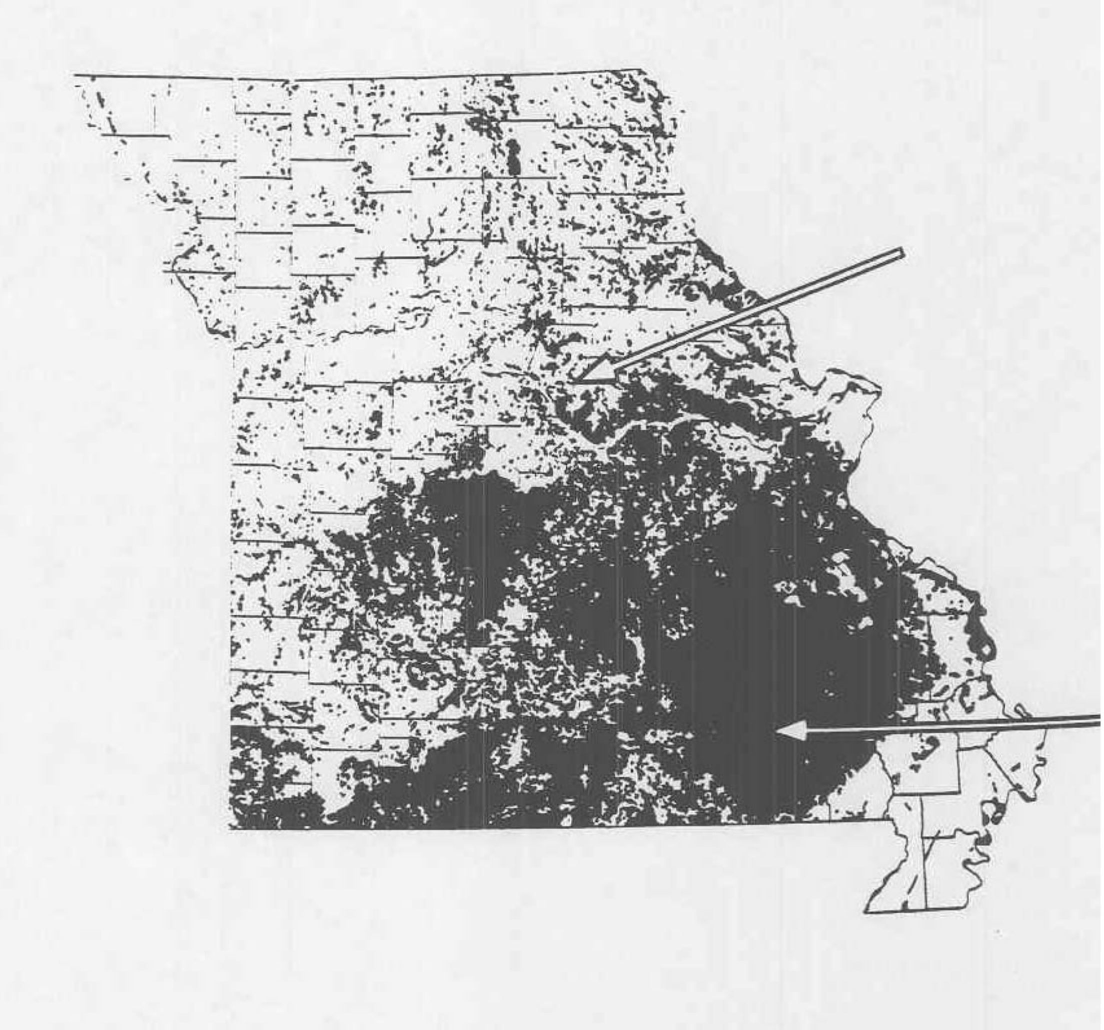


Figure 2. Images of a fragmented central Missouri study site (top) and a contiguous forest southeast Missouri study site (bottom) showing the forest cover (shaded) within 1, 3, 5, and 10 km radius circles.

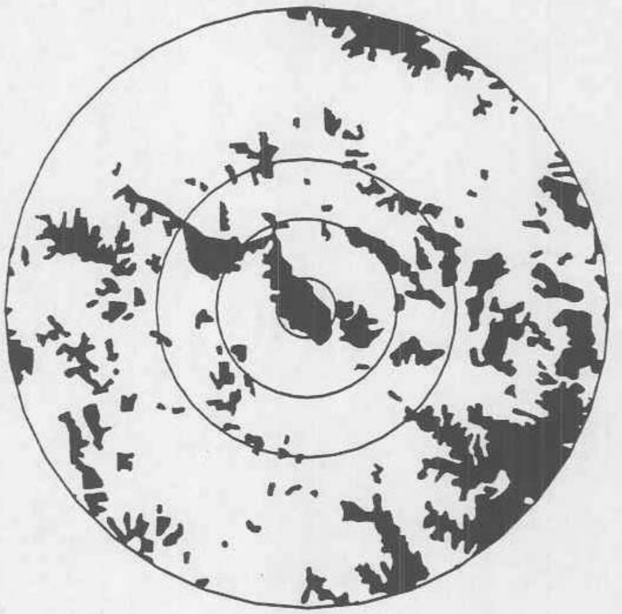


Figure 3. Relationship between cowbirds (male and females) and hosts on fragmented study plots in central Missouri. Cowbird abundance = .15 (number of hosts) + .096; F = 9.59; P = 0.0074; R^2 = .39. Because cowbird abundance varied with years, the relationship of cowbirds to hosts was calculated separately for each year (n = 9 plots in 1991 and 8 plots in 1992).

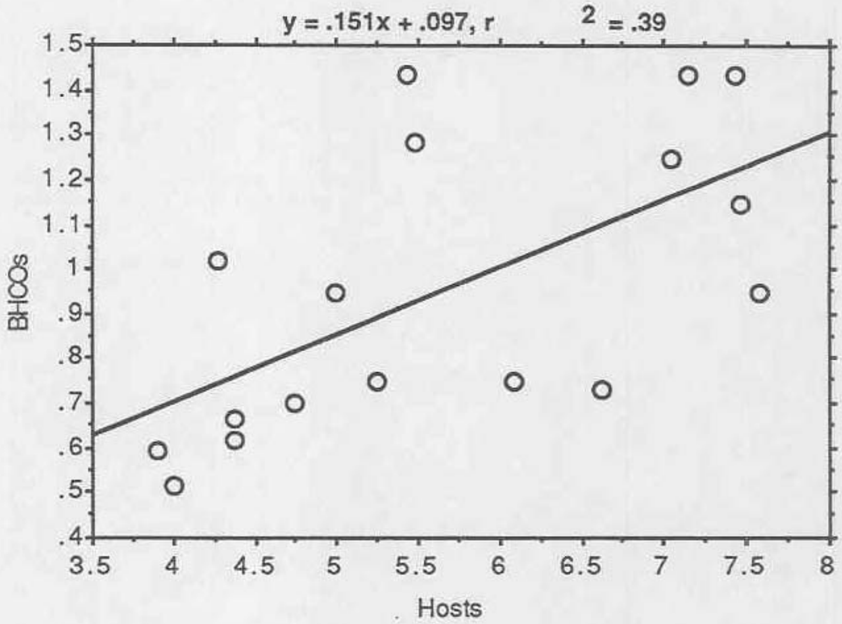
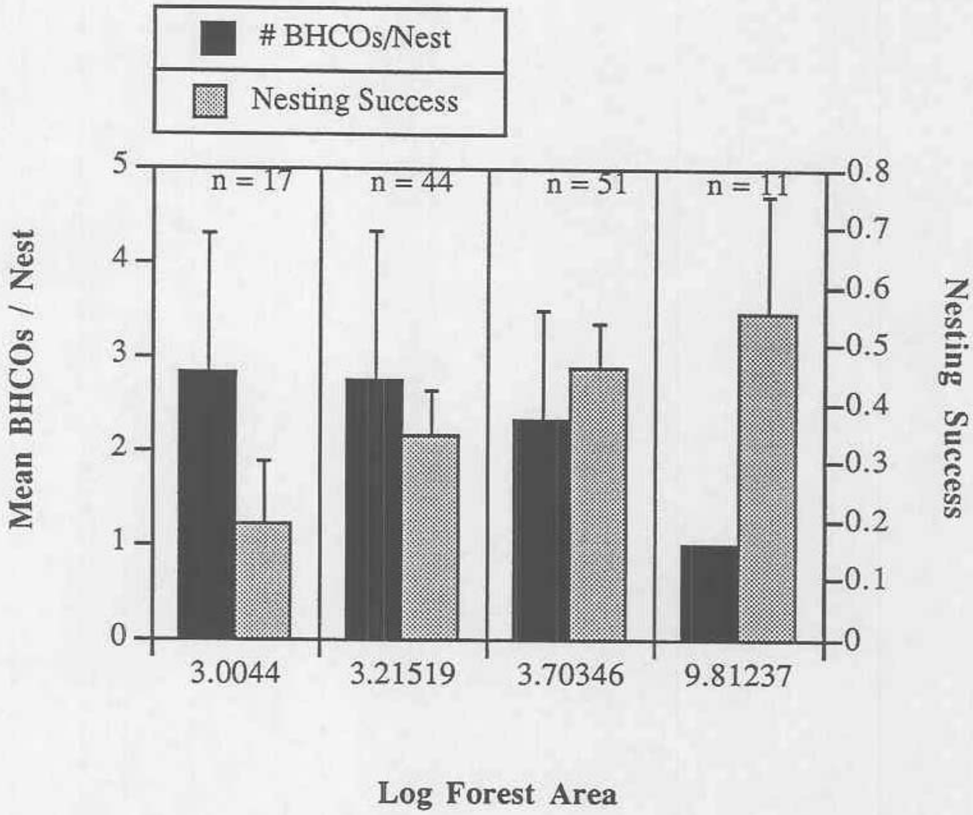

y = .151x + .097, r 2 = .39
BHCOs
1.5
1.4
1.3
1.2
1.1
1
.9
.8
.7
.6
.5
.4
3.5
4
4.5
5
5.5
6
6.5
7
7.5
8
Hosts

Figure 4. Solid bars show nesting success and standard errors of cowbirds on forests of different areas. Stipled bars show the mean number and standard deviation of cowbirds per parasitized nest on forests of different areas.



■ # BHCOs/Nest
▨ Nesting Success
Mean BHCOs / Nest
Nesting Success
0
1
2
3
4
5
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
n = 17
n = 44
n = 51
n = 11
3.0044
3.21519
3.70346
9.81237
Log Forest Area

Table 1. Description of the 7 forest tracts containing 17 study plots. Forest types are fragmented plots (frag) within central Missouri or contiguous plots (cont) within the Ozark region. "Plots" is the number of study plots situated within a particular forest tract; "sites" is the number of sites within a forest tract. Area units are km^2.

Forest	Plots	Sites	Type	Area (km^2)	Perimeter (km)	P:A	Forest Area r = 1 km	Forest Area r = 3 km	Forest Area r = 5 km	Forest Area r = 10km
Ashland	2	1	frag	40.6	142.5	3.5	2.5	18.9	41.4	132.3
Bennitt	1	1	frag	20.2	51.9	2.6	3.1	17.8	41.4	114.9
County J	2	1	frag	7.9	37.1	4.7	1.4	7.7	22.4	72.7
Fulton	1	1	frag	7.4	32.7	4.4	2.3	6.3	15.0	63.2
Hungry Mother	1	1	frag	24.9	82.2	3.3	2.5	16.8	37.1	103.1
Whetstone	2	1	frag	39.0	150.8	3.9	2.6	14.0	28.6	105.9
Ozarks	8	4	cont	18258.2	16842.9	0.9	3.1	27.3	75.7	289.4

Table 2. Repeated measures analysis of variance results using mean cowbird detections (female and male observations), mean female BHCO detections, and mean host detections at a study plot. Main effect of landscape is shown.

	FRAGMENTS			CONTIGUOUS			
Variable	Mean	SD	N	Mean	SD	N	P
Mean BHCO	0.95	0.32	17	0.27	0.12	14	.0001
Mean Female	0.20	0.12	17	0.04	0.02	14	.0001
Mean Host	5.66	1.32	17	6.88	0.78	14	.0042

Table 3. Univariate regressions of cowbird abundance, female cowbird abundance, and host abundance at a site (n = 10) against percent forest cover and perimeter to area ratios at selected spatial scales.

Dependent Variable	Independent Variable	Scale	Slope	Adj. R^2	P-value
BHCO Abundance	% Forest Cover	1 km	-1.503	.266	.0730
		3 km	-1.059	.670	.0023
		5 km	-1.106	.773	.0005
		10 km	-1.463	.854	.0001
	Perimeter/ Area Ratio	1 km	+.154	.189	.1166
		3 km	+.126	.547	.0087
		5 km	+.127	.685	.0019
		10 km	+.129	.773	.0005
Female BHCO Abundance	% Forest Cover	1 km	-.534	.678	.0021
		3 km	-.303	.939	.0001
		5 km	-.296	.933	.0001
		10 km	-.366	.850	.0001
	Perimeter/ Area Ratio	1 km	+.053	.480	.0158
		3 km	+.039	.900	.0001
		5 km	+.036	.905	.0001
		10 km	+.033	.839	.0001

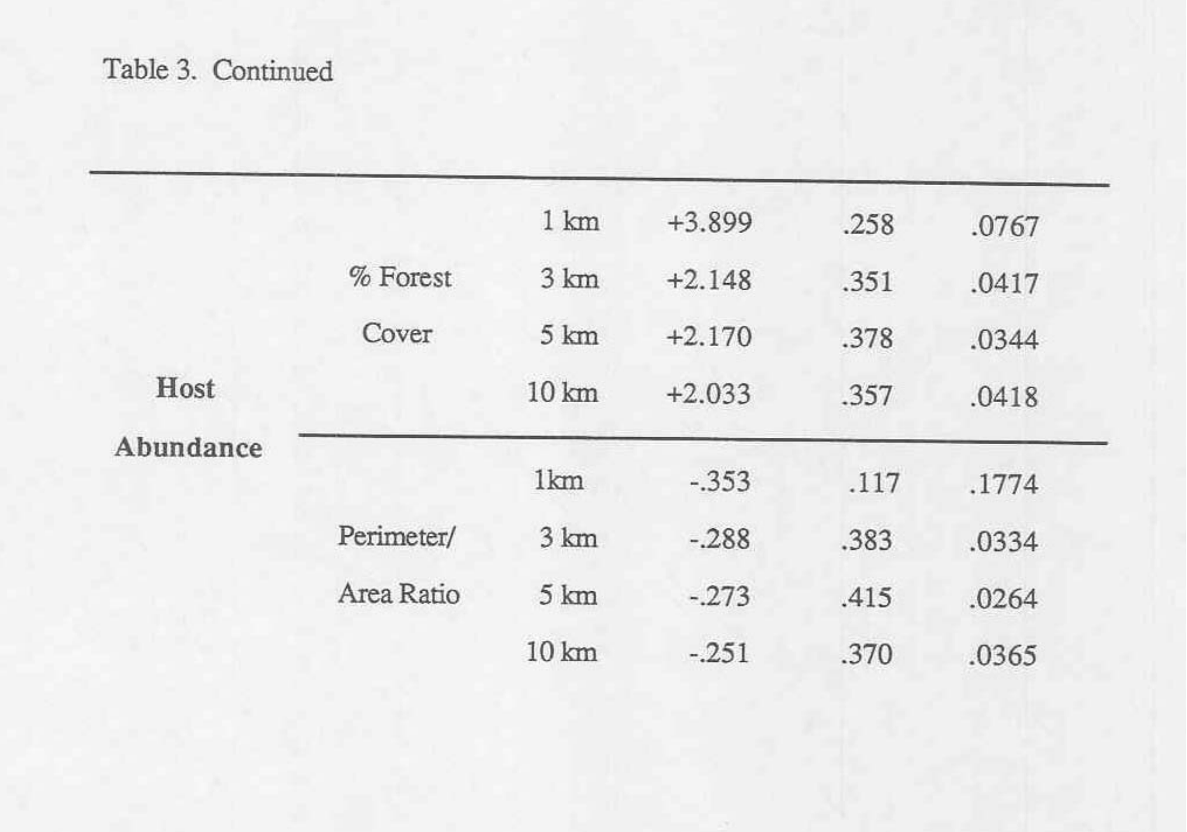


Table 3. Continued

Host Abundance	% Forest Cover	1 km	+3.899	.258	.0767
		3 km	+2.148	.351	.0417
		5 km	+2.170	.378	.0344
		10 km	+2.033	.357	.0418
	Perimeter/ Area Ratio	1km	-.353	.117	.1774
		3 km	-.288	.383	.0334
		5 km	-.273	.415	.0264
		10 km	-.251	.370	.0365

CHAPTER II

EFFECTS OF VEGETATION AND PREDATOR SPECIES ON NEST PREDATION PATTERNS IN FOREST FRAGMENTS

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ABSTRACT

The probability that a bird nest will successfully fledge young often depends on its proximity to a habitat edge. We experimentally determined if edge effects influence depredation rates of artificial nests on four forest fragments in the Saint Croix River Valley, Minnesota and Wisconsin, USA, and determined when these effects are most pronounced within a breeding season. We then assessed whether edge effects are due to differences in nest-site microhabitat or differences in predator communities by using cameras to identify nest predators in edge and interior habitats. On all four fragments, the probability of predation was higher near forest-field edges than nests in the forest interior (>200 m from any edge, $P = 0.0148$). Nest predation was higher late in the breeding season than early in the season ($P = 0.0144$). Nest site microhabitat influenced the probability of depredation in the forest interior ($P = 0.0044$), but not in edge habitat ($P = 0.095$), despite the fact that nests along edges were more concealed ($P = 0.031$). We identified four mammal and one bird species as nest predators. Raccoons (Procyon loter) were the most frequent predator,

depredating over 75% of nests that were monitored with cameras. These results suggest that ground-nesting birds in edge-dominated forests may experience decreased nesting success compared to birds that nest in contiguous forests with low interspersion of field habitat.

INTRODUCTION

Nest predation is the single most important cause of nest failure in migratory passeriformes (Martin 1992). The frequency and occurrence of nest predation has been linked to the spatial characteristics of a habitat (reviewed by Paton 1994). In general, nest predation rates are higher within 50 m of a habitat edge, defined as the juxtaposition of two different habitat types. Nest predation may be higher along habitat edges for two reasons. First, mammalian and avian nest predators may focus their nest searching activities along habitat edges, thereby increasing the probability of encountering and depredating a nest (Angelstam 1986, Yosef 1994).- Second, increased sunlight and wind along edges may alter the vegetation structure and nest-site microhabitat quality (Ambuel and Temple 1983), and these alterations may increase the probability that a nest will be depredated (Martin 1992).

Although the patterns of nest predation have been fairly well documented in both forested and unforested habitats (Paton 1994), edge effects appear to vary regionally and may depend on the local predator community (Andren and Angelstam 1988, Ratti and Reese 1988). Rather than simply documenting whether edge effects exist as a general pattern, information is needed to elucidate when edge effects exist and why edge effects exist; regional variation in these patterns should also be explored. Unresolved questions include the determination of the predator communities responsible for edge effects, the influence of nest-site microhabitat on nest predation patterns, and whether edge effects are constant throughout the breeding season.

Our objectives were to investigate 1) whether edge effects exist in the St. Croix River Valley, Minnesota and Wisconsin, USA, 2) if these effects vary from forest to forest, and 3) if these effects vary within the breeding season. To elucidate the results of the first three objectives, we identified interior and edge nest predators to understand whether nest predators are focusing their activities within each habitat type and if the predator community differed between edge and interior habitat. In addition, we compared nest-site microhabitat measures between edge and interior habitats to determine whether or not microhabitat influenced the probability of depredation.

STUDY AREA

We conducted our study in June and July 1992 in the Saint Croix River Valley, Minnesota and Wisconsin, USA. We studied nest predation on four study sites: William O'Brien State Park (MN; 5008325E, 516495N), Saint Croix Wild River State Park (MN; 5040990E, 520700N), Interstate State Park (WI; 5026320E, 529435N), and a private landholding located adjacent to the Wild Mountain Ski and Recreational Area (MN; 5036810E, 522150N). All sites were forest fragments located within an agricultural landscape. Sites ranged from approximately 80 to 160 ha of contiguous forest. These sites were relatively mature deciduous forests, and edge and interior habitat was of comparable forest structure and composition (Donovan, unpubl. data.). Dominant canopy species included sugar maple (Acer saccharum), basswood (Tilia americana), red oak (Quercus rubra), white ash (Fraxinus americana), slippery elm (Ulmus fulva), and black cherry

(Prunes serotina). Understory tree and shrub species included ironwood (Carpinus caroliniana), hazelnut (Corylus americana), and prickly ash (Zanthoxylum americanum).

METHODS

Experimental Design

To test our hypotheses, we conducted field experiments on all four study sites using artificial nests. Artificial nests have been extensively used to elucidate how nest predation rates vary spatially across a habitat (Paton 1994). Although depredation rates on artificial nests may not be highly correlated with depredation on natural nests (Reitsma et al. 1990), artificial nests may provide an estimate of relative predation rates (Paton 1994).

Our objectives were to determine if predation rates on artificial nests varied among sites, spatially within a site, and across time throughout the breeding season. We refer to edge effects as the difference in depredation rates between edge habitat (<50 m from a habitat edge) and interior habitat (>200 m from a habitat edge). We refer to timing effects as the difference in depredation rates on nests in early June and on nests in late June (see I below), and refer to site effects as the difference in depredation rates among the four study sites. We used a 3-way analysis-of-variance factorial -design to simultaneously test for edge effects, timing effects, and site effects (n = 15 nests per cell; N = 240). Two nests were inadvertently lost, reducing the total artificial nest sample size to 238. The factorial experimental design allowed us not only to test for edge, timing, and site effects, but also to test for interactions among those effects, i.e., to determine if one effect varied depending on another effect.

Within each study site, we designated suitable forest interior (>200 m from an abrupt ecotonal edge) and forest edge habitat (<50 m from an abrupt ecotonal edge). These distances were appropriate because most edge effects in similar forests usually occur within 50 m from an edge (Paton 1994). Internal edges within a forest that created a break in canopy coverage, such as hiking trails, were excluded from sampling. In each site, we randomly placed fifteen artificial nests in the designated edge habitat and fifteen artificial nests in the designated interior treatment. Within each habitat type, we separated all artificial nests by a minimum of 50 m. This distance reduced the probability that a small number of predators were responsible for all depredations (Laurance and Yensen 1991), but also reflected the density of ground-nesting species where our study was conducted (Donovan, unpubl. data).

The protocol described above was conducted in two separate 14 day trials to test for timing effects (Table 1). We sampled Trial 1 in early June (5 June - 18 June) and sampled Trial 2 in late June (19 June - 3 July). Within each 14 day trial, we conducted experiments on all four sites. Because of time and man-power constraints, we conducted experiments on two sites during the first seven days in each trial, and conducted experiments on the remaining two sites during the last seven days in each trial. We began Trial 1 when it appeared that most ground-nesting female passerines were incubating their first clutch. Trial 2 simulated either a female's second attempt after an initial nest failure or a late first nesting attempt.

Artificial Nest Protocol

We used commercial canary wicker baskets (10.5 cm wide and 5.5 cm deep) as artificial nests. Each nest was placed directly on the ground and partially concealed with leaf and grass litter to simulate a generic ground nesting Neotropical migrant warbler

(Wilcove 1985). We baited each nest with two quail (Colinus virginianus) eggs, and subsequently checked and scored as depredated or not depredated seven days later. We wore latex gloves to reduce human scent while handling quail eggs, and minimized contact with eggs and vegetation. We scored nests as depredated if one or both eggs were absent or destroyed.

Nest-Site Microhabitat Measurements

We measured two microhabitat vegetation variables at each artificial nest site. We measured overhead cover as the percent of vegetation cover in a 25 cm diameter cylinder within 1/2 m above the nest. We estimated side cover in a 25 cm diameter cylinder within one meter of the nest in each of the four cardinal directions, and used the mean of the four side cover estimates in statistical analyses.

Camera Documentation of Nest Predators

In conjunction with the artificial nest experiments, we used 10 Cam-Trakker (CAM-TRAKKER, D. Stonebumer, Athens GA), 35 mm cameras to document nest predators of edge and interior artificial nests. Cameras were equipped with a passive infrared motion detector, designed to detect heat in motion __<18 m. Each camera had an automatic flash to detect nocturnal predators and automatic film advance that stamped the date and time on the film.

We monitored each site using cameras for seven days (Table 1). For a given site, we randomly selected 5 edge and 5 interior nests to be simultaneously camera-monitored. We placed cameras on a tree at a distance of 1-4. m and focused cameras toward the nests. If a camera-monitored nest was depredated by Day 4, we randomly selected another nest within the same treatment to be camera- monitored until Day 7.

We photographed many animals, but not all photographs were considered predation events. For example, browsing or roaming white-tailed deer (Odocoileus virginianus) frequently triggered cameras. Photographed animals were considered nest predators if they were caught in the act of depredating eggs or if, upon examination, eggs were missing and no other animal was photographed at the nest.

STATISTICAL ANALYSES

Edge, Timing, and Site Effects

We tested whether the probability of depredation differed between habitats (edge vs interior), between trials (trial 1 vs trial 2), and among sites, plus all interactions using a categorical analysis-of-variance model (CATMOD procedure, SAS Institute Inc.). This test is very similar to an analysis-of-variance but uses categorical data (depredated or not depredated) as the dependent variable (SAS Institute Inc.).

To test whether the probability of depredation depended upon habitat type (edge vs. interior), we pooled observations across time periods and sites. Each habitat type (edge vs interior) therefore contained n =119 nests. To determine whether the probability of depredation varied among sites, we pooled observations across time periods and habitat types. Each site therefore contained n = 60 nests (Table 1). To determine whether the probability of depredation varied within a nesting season, we pooled observations across treatments and sites to analyze timing effects. Each trial therefore consisted of n =120 W nests (Table 1).

In addition to testing for edge, timing, and site effects, we tested for all interactions among these effects. We used a Type I error rate of 0.05 for all analyses.

Effects of Nest-Site Microhabitat

Because overhead cover and side cover vegetation measurements were correlated (R = 0.466, P = 0.001), and because they both empirically measured the degree to which nests were concealed, we used a multivariate analysis of variance (Wilkes' Lambda) to test the null hypothesis that edge and interior nests were equally concealed. Overhead and side cover were the two dependent variables, and treatment (edge vs. interior) was the independent variable.

We used logistic regression to determine if there was a linear relationship between nest concealment and probability of depredation. Logistic regression is similar to linear regression in that the independent variable is a continuous variable, but the dependent variable is categorical. In logistic regression, categorical data (such as depredated or not depredated) is transformed to an expected value of y given x, and maximum likelihood estimators are used to estimate parameters which maximize a function that agrees most closely with the observed data (Hosmer and Lemeshow 1989). For this analysis, we used overhead cover, loosely interpreted as "cover" because of its correlation with side cover, as the independent variable. We transformed the categorical data (depredated or not depredated) to the probability of depredation, and used this probability as the dependent variable.

RESULTS

Edge, Timing, and Site Effects

We detected differences in depredation rates between treatments, trials, and sites (Table 2). Nests set in late June (Trial 2) were more likely to be depredated than nests set in early June (Trial 1, P = 0.014, Table 2). Edge nests were more likely to be depredated than interior nests (P = 0.015, Table 2 and Figure 1). We detected differences in depredation among sites (P = 0.0001, Table 2). Nests at Interstate State Park had a higher probability of depredation compared to the other three sites (Figure 1). There were no interactions in the categorical analysis-of-variance model (Table 2, P> 0.35).

We assessed adequacy of a main-effects model by examining the maximum likelihood predicted values for the response function and frequencies. Inclusion of the interaction .terms in the full model did not improve the goodness-of-fit, therefore a main effects model was appropriate.

Effects of Nest-Site Microhabitat

Overhead and side cover were positively correlated with each other (R = 0.47, P = 0.0001). Edge nests were more concealed by edge and side cover than interior nests (F = 3.50, 2,233 df, P = 0.031), but this concealment affected the probability of depredation differently in the two different habitats. For interior nests, the probability of depredation decreased by 2.5% for every 10% increase in the amount of overhead cover (odds ratio = 0.98, P = 0.007, Figure 2). For edge nests, an increase in overhead cover tended to reduce the probability of depredation, but this relationship was not significant at the 0.05 level (P = 0.095; Figure 2).

Camera Documentation of Predators

Twenty-seven photographs of predators depredating an artificial nest were obtained, including both avian and mammalian predators (Figure 3). We photographed more predators in edge habitat than interior habitat. Photographed predators included the raccoon (Procyon lotor) , eastern grey squirrel (Sciurus carolinensis), American crow

(Corvus brachyrhynchos), striped skunk (Mephitis mephitis), and the white-tailed deer (Odocoileus virginianus). Similar predators were photographed depredating both interior and edge artificial nests. Raccoons were the dominant nest predator in both edge and interior habitat, but were observed depredating twice as many edge nests as interior nests (Figure 3).

DISCUSSION

Edge Effects

Artificial nests located along edges had higher depredation rates than interior nests, and our study revealed two unique insights into edge-related predation. First, most artificial nest studies identified birds (primarily Corvids) as the dominant nest predators (see Paton 1994 for review), whereas we determined that raccoons were the most frequent nest predator, depredating over 75% of all nests that were monitored with cameras. Second, raccoons were photographed depredating twice as many nests in edge habitat compared to interior habitat. We were unable to ascertain what factors account for high raccoon depredation along edges and whether or not specific individuals focused their feeding activities along edges. These factors may depend on age, sex, time of year, and experience of the animal (Greenwood 1982). More detailed studies of predator feeding behavior in relation to habitat patterns are needed to determine if different types of predators search for food differently in edge and interior habitats.

Site Effects

Although the four sites were of similar size and had similar forest composition and structure, nests at Interstate State Park had a higher probability of depredation compared to the other three sites. This is noteworthy because three of the sites were State Parks with active camping facilities (>100 campsites). Two of those sites, William O'Brien State Park and Wild River State Park, utilized animal-proof dumpsters for visitor garbage for at least 10 years prior to the study (D. Crawford, pers. comet.). By contrast, Interstate State Park utilized over 100 individual garbage cans associated with campsites that were regularly visited by raccoons (J. Fox-Martin, pers. comet.). The single-can system was utilized until the spring of 1992 when both a dumpster system and our study were initiated. Raccoon populations probably benefited from the single can system, but were perhaps forced to find natural food sources when the dumpster policy began. The predominance of raccoon predation attempts and the high nest-mortality at Interstate State Park support this notion.

Timing Effects

Our data showed that artificial nests initiated in late June had higher predation rates and than nests set in early June. Our artificial nests simulated only the incubation period of ground nesting species, so we could not determine whether the intensity of nest predation varied during other stages of the nesting cycle. These results were also demonstrated by Burger et al. (1994) and Carlson and Faaborg (unpubl. manuscript). Recent studies have documented that males in edge-dominated forest fragments establish territories later in the season than males in unfragmented habitats (Wander 1985; Gentry 1989). If this late settlement results in delayed pairing and incubation, then nest survival may decrease because predation on eggs increases later in the breeding season. Our results indicate that increased predation pressures later in the breeding season were pronounced in both edge and interior habitats and in all four sites. Thus, the timing of nest predation did not appear to be governed by the occurrence of edge, and future research should focus on identifying factors that influence the timing of nest initiation.

Microhabitat Effects

We discovered that direct overhead cover at a nest is related to whether or not a nest is depredated, but the strength of this relationship depends upon nest location. For interior habitat nests, as overhead cover increased the probability of depredation decreased. However, overhead cover in edge nests only weakly affected the probability of being depredated, even though edge nests were more concealed with vegetation than interior nests. The importance of nest concealment in avoiding predation may very well depend on the predator community. It has been suggested that artificial nest experiments are biased toward avian predators, species which use visual cues to locate nests (Willebrand and Marcstrom 1988). If avian predators were common in our study area, we would predict that increased nest concealment would decrease the probability of predation. Indeed, increased nest concealment did reduce the probability of depredation, but only in interior habitats. However, we determined that raccoons were the most frequent nest predator along habitat edges, and studies of raccoon foraging behavior show that the degree of nest cover is much less important in preventing depredation than local habitat heterogeneity (Bowman and Harris 1980). Many mammalian predators rely on olfactory cues to locate their prey, and therefore the probability of predation may be irrespective of visual concealment (Grant and Morris 1971). If raccoons use primarily olfactory cues and focus their searching along habitat edges, increased nest concealment may play a weak role in reducing the probability of nest predation.

Management Implications

Nest predation rates are higher along habitat edges in the St. Croix River Valley, and may be due to increased raccoon feeding behavior along edges. Because raccoons and other mammals use olfactory cues in locating their prey, management for nest-site microhabitat may not relieve edge effects in the St. Croix River Valley. Our study is unique among other artificial nest studies in that most studies confirm that Corvids are the primary nest predator. In those study regions, management for nest-site microhabitat may reduce edge effects if an increase in cover results in a decrease in Corvid predation. We suggest that knowledge of the predator community is the first step toward understanding why edge effects exist and why these effects appear to vary regionally.

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LITERATURE CITED

Andren, H., and P. Angelstam. 1988. Elevated predation rates as an edge effect in habitat islands: Experimental evidence. Ecology 73:794-804.

Angelstam, P. 1986. Predation on ground-nesting birds' nests in relation to predator densities and habitat edge. Oikos 47:365-373.

Ambuel, B., and S. A.Temple. 1983. Area dependent changes in the bird communities and vegetation of southern Wisconsin forests. Ecology 64:1057-1068.

Bowman, G. B., and L. D. Harris. 1980. Effect of spatial heterogeneity on ground-nest depredation. J..Wildl. Manage. 44:806-813.

Burger, L. D., L. W. Burger, and J. Faaborg. 1994. Effects of prairie fragmentation on predation on artificial nests. J. Wildl. Manage. 58:249254.

Gentry, R. 1989. Variable mating success of the Ovenbird (Seiurus aurocapillus) within remnant forest tracts of central Missouri. M.A. Thesis, Univ. Missouri, Columbia.

Grant, P. R., and R. D. Morris. 1971. The distribution of Microtus pennsylvanicus within grassland habitat. Can. J. Zool. 49:1043-1052.

Greenwood, R. J. 1982. Nocturnal activity and foraging of prairie raccoons (Procyon lotor) in North Dakota. Am. Midl. Nat. 107:238 233.

Hosmer, D. W., and S. Lemeshow. 1989. Applied logistic regression. John Wiley and Sons, New York.

Laurance, W. F., and E. Yensen. 1991. Predicting the impacts of edge effects in fragmented habitats. Biol. Conserv. 55:77-92.

Martin, T. E. 1992. Breeding productivity considerations: what are the appropriate habitat features for management? Pages 455-473 in Ecology and conservation of Neotropical migrant landbirds (J. M. Hagan III and D. W. Johnson, eds.). Smithsonian Institute Press, Washington D.C.

Paton, P. 1994. The effect of edge on avian nest success: how strong is the evidence? Conserv. Biol. 8:17-26.

Ratti, J. T., and K. P. Reese. 1988. Preliminary test of the ecological trap hypothesis. J. Wildl. Manage. 52:484-491.

Reitsma, L. R., R. T. Holmes, and T. W. Sherry. 1990. Effects of removal of red squirrels, Tamiasciurus hudsonicus, and eastern chipmunks, Tamias ltd=, on nest predation in a northern hardwood forest: An artificial nest experiment. Oikos 57:375-380.

SAS Institute Inc. 1990. SAS user's guide: statistics, version 6 edition. SAS Institute Inc., Cary, North Carolina.

Wander, S. A. 1985. Comparative breeding biology of the ovenbird in large vs. fragmented forests: implications for the conservation of Neotropical migrant birds. Ph.D. Dissertation, Rutgers Univ., New Jersey.

Wilcove, D. S.,1985. Nest predation in forest tracts and the decline of migratory songbirds. Ecology 66:1211-1214.

Willebrand, T., and V. Marcstrom. 1988. On the danger of using dummy nests to study predation. Auk 105:378-379.

Yosef, R. 1994. The effects of fencelines on the reproductive success of loggerhead shrikes. Conserv. Biol. 8:281-295.

Figure 1. Predation rate on artificial nests in edge (solid bar) and interior (open bar) habitat in four sites; INT = Interstate State Park, O'B = William O'Brien State Park, W.M. = Wild Mountain, WR = Wild River State Park.

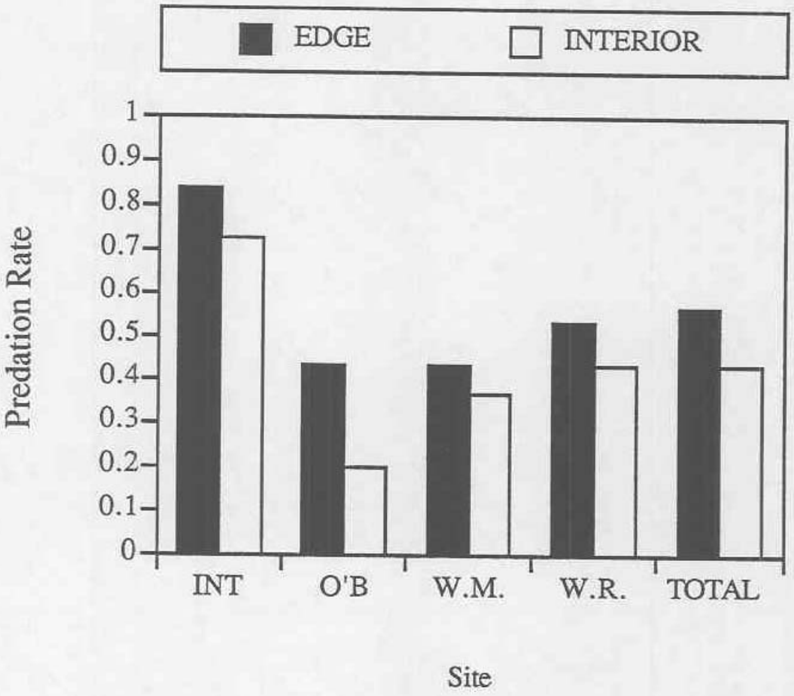
EDGE
INTERIOR
Predation Rate
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
INT
O'B
W.M.
W.R.
TOTAL
Site

Figure 2. The logistic regression functions for edge and interior nests. The logit function for interior nests shows that the probability of depredation decreases as the overhead cover increases, while there is no a relationship between overhead cover and the probability of depredation for edge nests.

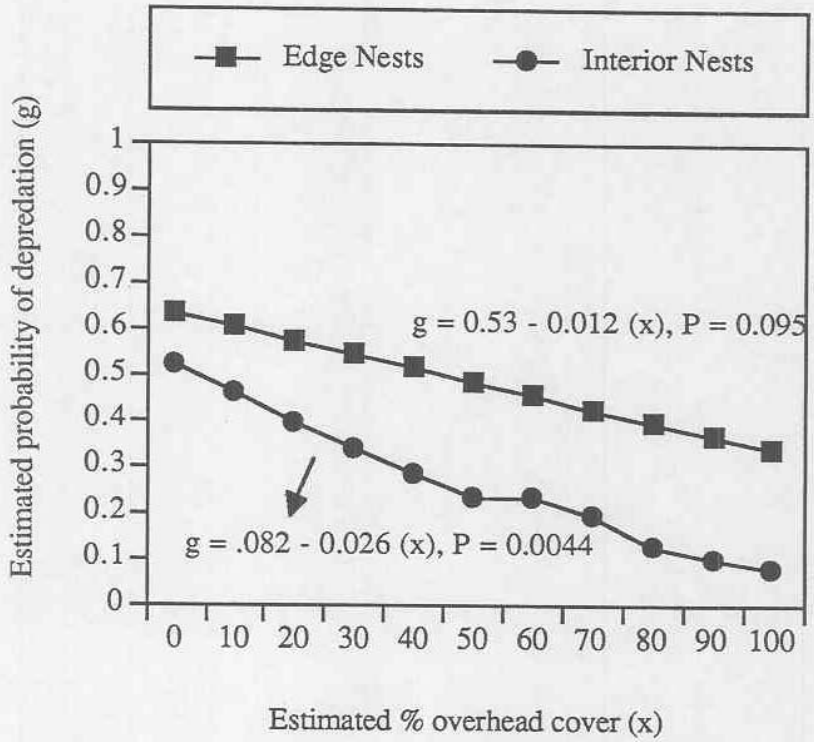
Edge Nests
Interior Nests
Estimated probability of depredation (g)
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
g = 0.53 - 0.012 (x), P = 0.095
g = .082 - 0.026 (x), P = 0.0044
0
10
20
30
40
50
60
70
80
90
100
Estimated % overhead cover (x)

Figure 3. Number of filmed predation events for known predators in both edge and interior habitat.

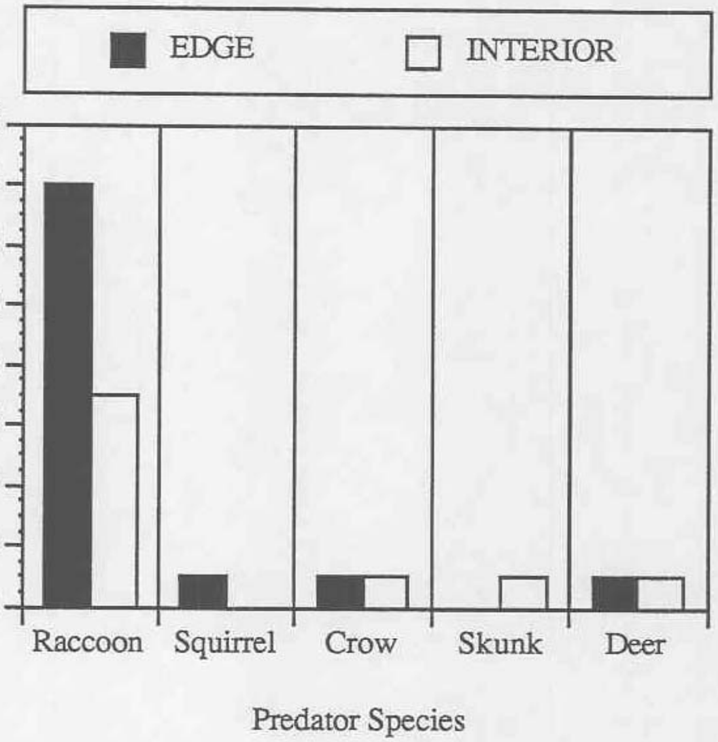
EDGE
INTERIOR
Number of predation events.
16
14
12
10
8
6
4
2
0
Raccoon
Squirrel
Crow
Skunk
Deer
Predator Species

Table 1. Experimental design of artificial nest study. X denotes both site and week in which a seven day artificial nest experiment was conducted. For each X, 15 nests were placed in edge habitat and 15 nests were placed in interior habitat. X_{camera} denotes the site and week in which both edge and interior nest predators were photographed.

		O'Brien	**Wild Mtn.**	**Interstate**	**Wild River**
Trial 1	Week 1	X		X_{camera}	
	Week 2		X_{camera}		X
Trial 2	Week 1		X		X_{camera}
	Week 2	X_{camera}		X	

Table 2. Maximum-likelihood analysis-of-variance results. The probability that depredation differs between main effects of treatments (edge vs. interior), trials, and sites was tests, and interactions among main effects were tested.

Source	df	Chi-Square	P
Treatment	1	5.94	0.0148
Trial	1	5.99	0.0144
Site	3	25.67	0.0001
Treat*Site	3	1.95	0.5831
Treat*Trial	1	0.04	0.8370
Trial*Site	3	3.04	0.3856
Treat*Trial*Site	3	2.49	0.4770

CHAPTER III

A NEW METHOD OF DETERMINING OVENBIRD AGE BASED ON RECTRIX SHAPE

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ABSTRACT

Understanding age-specific differences in life history characteristics depends on accurate assessment of age. We investigated the use of rectrix shape for aging Ovenbirds (Seiurus aurocapillus) as HY/SY or AHY/ASY individuals. We used a microscope, a videocamera, and image analysis software to analyze rectrix tip angles of 82 birds of known age. AHY/ASY birds had larger tip angles than HY/SY birds ($P = 0.0001$) and birds were correctly classified into their correct age-class over 90% of the time. Our method of quantifying rectrix shape was time efficient and accurate.

INTRODUCTION

Many bird species exhibit age-related differences in fecundity, mortality, habitat use, and social dominance. The Ovenbird (Seiurus aurocapillus) is a forest-nesting warbler whose breeding and biology has been relatively well studied (Van Horn and Donovan, 1994). Their ground-nesting behavior in the summer and ground-feeding behavior during summer, winter, and migration facilitate capture and observation for testing life history hypotheses. Despite these qualities, age-related differences in habitat use, breeding success, and site fidelity have not been studied in Ovenbirds because many cannot be reliably aged 5 months after fledging (Pyle et al. 1987).

Here, we investigate the potential of using rectrix shape to age breeding Ovenbirds as first-year breeders (SY birds) or older breeders (ASY birds) and wintering Ovenbirds as first-year birds (HY/SY) or older birds (AHY/ASY). Immature (HY/SY) Ovenbirds undergo a partial first prebasic and prealternate molt; their tail feathers are retained throughout their first winter season and are not molted until after their first breeding attempt (Pyle et al. 1987). Thus, a first-year breeder (SY) has the same rectrices it acquired immediately after hatching. These rectrices often are worn and tapered in shape (Pyle et al. 1987). By contrast, older birds (AHY/ASY) undergo a complete second pre-basic molt, where all flight feathers and rectrices are replaced after the breeding season but prior to fall migration. The newly acquired rectrices are less worn and paddle-shaped (Pyle et al. 1987). The difference in rectrix shape between the two age-classes are purportedly due to differences in development (Laaksonen and Lehikoinen 1976). Thus, an Ovenbird arriving on the breeding grounds or the wintering grounds for its second time or more has new rectrices that are less worn and are not distinctly tapered as those on a younger bird. This difference in molt phenology produces measurable differences in rectrix shape between first-year (HY/SY) birds and older (AHY/ASY) birds. These differences have been used in aging many other bird species (e.g., Meigs et al. 1983, Svensson 1984, Collier and Wallace 19$9). These measurable differences in rectrix shape can be perceived by visual examination by inexperienced banders (70-80% accuracy) and classification of birds to their correct age-class can improve with experience (Weinberg and Roth 1994).

In this paper, we: 1) describe a new method for measuring rectrix shape, 2) determine if HY/SY and AHY/ASY Ovenbirds differ measurably in rectrix shape, 3) determine the reliability of aging Ovenbirds based on rectrix shape, and 4) devise a function that can be used to age Ovenbirds in the field.

STUDY AREAS AND METHODS

We collected rectrix number 3 from 82 Ovenbirds of known age in 8 geographic locations in 1993 and 1994 (see below, Table 1). Seventeen rectrices were collected during the 1993 breeding season in the St. Croix River Valley (Minnesota) and in the Chequamegon National Forest (Wisconsin). Sixty rectrices were collected during fall migration (1993) at 5 banding stations: Long Point Bird Observatory (Ontario), Toronto Bird Observatory (Ontario), Manomet Bird Observatory (Massachusetts), Island Beach (New Jersey), and Bon Secour National Wildlife Refuge (Alabama). Five rectrices were collected during the winter (1994) in Guanica National Forest (Puerto Rico).

Age Determination of Ovenbirds

All birds were captured in mist nets, banded, and aged. During the breeding season before the prebasic molt, Ovenbirds can be aged as HY (young of the year) or AHY (adults, U.S. Fish and Wildlife Service and Canadian Wildlife Service 1980). However, we banded Ovenbirds in the Chequamegon National Forest and the St. Croix River Valley during the summers from 1991-1992, and breeding adults that were banded and subsequently recaptured in 1993 were classified as ASY individuals. Rectrices from 8 HY (young of the year) and 9 ASY birds were obtained during the breeding season (Table 1).

During fall migration, Ovenbirds can be aged as HY (young of the year) or MY (adult) birds. HY Ovenbirds have incompletely pneumitized skulls and rusty-edged tertials, whereas AHY Ovenbirds have completely pneumatized skulls and lack rusty-edged tertials (Taylor 1972, 1973). All AHY birds, however, have undergone their second prebasic molt and thus have new, paddle-shaped tail feathers. We classified all Ovenbirds I captured during migration without rusty tertials and with completely pneumatized skulls as AHY birds. Rectrices from 36 HY and 24 AHY birds were obtained during fall migration (Table 1).

On the wintering grounds, Ovenbirds often cannot be reliably aged because both young and old birds usually have completely pneumatized skulls. In the Guanica National Forest, Ovenbirds have been captured and banded during January since 1972 (Faaborg and Arendt 1992). Birds that were banded prior to 1994 and subsequently recaptured in 1994 were classified as ASY birds. Rectrices from 5 ASY wintering birds were obtained ('Table 1).

Quantifying Differences in Rectrix Shape

Although rectrices were obtained from birds of known age, we quantified differences in rectrix shape "blindly," that is, without immediate knowledge of age. We smoothed each feather to its natural contour, and placed it under a Bausch & Lomb microscope. We acquired images of each rectrix with a Videoscope CCD 200E camera (Video Scope International, Washington, D.C.) attached to the microscope. We illuminated the feathers from above using a dual-fiber light source. The camera was attached to a computer which was calibrated for the scope's magnification. We saved the images and analyzed them using Image-1 (Universal Imaging Corp., West Chester, PA) image analysis software.

We used the Image-1 program to place a 1.5 mm grid of calibrated distances over the image of the feather. The grid was aligned along the feather rachis and centered on the feather tip (Figure 1). We obtained the rectrix tip angle following methodology described in Meigs et al. (1983) and Collier and Wallace (1989). Beginning at the rectrix tip and moving across the inner vane, we measured 1.5 mm perpendicular to the rachis and then down to the point where the feather intersected the 1.5 mm grid line that paralleled the rachis (Figure 1). We used the "measure distance" function in Image-1 to obtain an angle for the line segment beginning at the rectrix tip and ending at the feather-grid-intersection. We repeated this procedure on the outer vane portion of the feather, obtaining angle measurements for two line segments per feather. The difference between these angles was computed and defined as the tip angle. We repeated the entire process four times for each feather. Randomly chosen feathers were also measured by both investigators to check for observer consistency.

We used the mean of the four measurements for each feather to compute the mean tip-angle for each age class. Differences among age classes in mean tip angle were tested using an analysis of variance (Sokal and Rohlf 1981). We determined discriminant equations to classify birds, and determined the accuracy of aging Ovenbirds based on rectrix shape by using a discriminant function cross-validation analysis (Pros Discrim, SAS Institute Inc. 1990).

Tolerance Intervals

Because there is some probability of misclassification using the discriminant function approach, we constructed tolerance limits using the mean feather tip-angles, sample sizes, and mean within-group variance from the analysis of variance (Wald and Wolfowitz 1946). The tolerance intervals allow nearly 100% accuracy in classification by eliminating any rectrices that could potentially be misclassified, and thus are a more conservative approach to classifying Ovenbirds based on rectrix shape. The equation, x ± ~ (s.e.) defines the tolerance intervals by which Ovenbirds can be classified as HY/SY or AHY/ASY birds, where "x" is the mean tip angle for each age class, "s.e." is the standard error for each age class, and "0" is the tolerance value. We used 99 and 99.9 tolerance values, which means we are 99% confident that the tolerance limit includes 99.9% of the angles of each age group.

RESULTS

Age Related Differences in Rectrix Shape

AHY/ASY Ovenbirds have larger tip angles (mean = 96.08, sd = 8.08) than HY/SY Ovenbirds (mean = 72.2, sd = 8.08; F = 165.53; P = 0.0001; R2 = 0.67; Figure 2). Two discriminant equations were derived to classify Ovenbirds based on tip angle:

If age = ASY, then ø = -65.73970 + x (1.36845)
If age = HY, then ø = -37.12789 + x (1.02841)

where x is the angle of a bird of unknown age. Substituting x in for both equations, the bird is classified into the age class of the equation that yields the highest score (0). Using these equations, 92.11% of the 38 ASY birds were correctly classified as ASY, and 90.91% of the 44 SY birds were correctly classified as SY. Of the birds that were misclassified, 4 HYs and 3 ASYs were classified as ASY and HY, respectively.

Tolerance Intervals

Ovenbirds can be classified as HY/SY or AHY/ASY by the following tolerance limits:

If tip angle, x, $\geq$ 90.05, then age = AHY/ASY;
If tip angle, x, $\leq$ 77.92, then age = HY/SY;
If 90.05 $\geq$ x $\geq$ 77.92, then age = AHY/U.

DISCUSSION

Using the two discriminant functions given above, breeding and wintering SY and ASY Ovenbirds can be reliably aged from tip-angles with over 90% certainty. Using tolerance limits described, Ovenbirds can be classified as HY/SY or AHY/ASY with over 99% certainty if tip angles are greater than 90° or less than 78°. If field workers can visually perceive tip-angle as >_90° or <_'78° (e.g., Weinberg and Roth 1994), then Ovenbirds potentially can be accurately aged without direct measurement of the rectrix. We believe that, with practice, most workers can perceive these differences.

The combination of a simple macroscope, computer, and image-analysis program allowed us to obtain rapid, reliable and extremely accurate tip-angle data. Once the system was in place, each feather could be measured four times in approximately 1 minute. Other investigators used paper grids for measurements, but we believe that working with a feather image, rather than the feather itself, helped reduce measurement error. The image could be moved on screen so that we could align the 1.5 mm grid precisely. Measurements made in this manner are very precise; our four measurements taken on a single feather usually did not differ by more than 1-3 degrees.

The Image-1 software package can perform a variety of tasks applicable to ornithological studies. Other software packages, such as NIH Image, are available via Shareware to most institutions in the U.S.

ACKNOWLEDGEMENTS

We are especially grateful to the staff and volunteers who collected rectrices while working on independent research projects. G. Krause helped compute the tolerance intervals. We thank G. Wallace, J. Faaborg, and F. Thompson In, who reviewed manuscript and helped clarify the sometimes confusing nomenclature used to describe birds of different ages. Helpful comments by C. Galen, M. Ryan, and R. Semlitsch improved the manuscript. This study was funded in part by the USDA Forest Service North Central Forest Experiment Station and the Minnesota Department of Natural Resources Nongame Wildlife Fund.

LITERATURE CITED

Collier, B., and G. E. Wallace. 1989. Aging Catharus thrushes by rectrix shape. J. Field Ornithol. 60:230-240.

Faaborg, J., and W. Arendt. 1992. Long-term declines of winter resident warblers in a Puerto Rican dry forest: Which species are in trouble? Pages 57-63 in Ecology and conservation of Neotropical migrant landbirds (J. M. Hagan and

D. W. Johnston, eds). Smithsonian Institution Press, Washington, D.C. Laaksonen, M., and E. Lehikoinen. 1976. Age determination of Willow and Crested Tits, Pares montanus and P cristatus. Ornis Fenn. 53:9-14.

Meigs, J. B., D. C. Smith, and J. Van Buskirk. 1983. Age determination of Black capped Chickadees. J. Field Ornithol. 54:283-286.

Pyle, P., S. N. G. Howell, R. P. Yunick, and D. F. DeSante. 1987. Identification guide to North American passerines. Slate Creek Press, Bolinas, California.

Taylor, W. K. 1972. Analysis of Ovenbirds killed in central Florida. Bird-Banding. 43:15-19.

--------- 1973. Aging Ovenbirds by rusty tipped tertials and skull ossification. EBBA News 36:71-72.

SAS Institute Inc. 1990. SAS/STAT User's Guide, version 6 edition. SAS Institute Inc., Cary, North Carolina.

Sokal, R. R., and F. J. Rohlf. 1981. Biometry. Freeman and Co., San Francisco, California.

Van Horn, M., and T. M. Donovan. 1994. Ovenbird (Seiurus aurocapillus). In The Birds of North America, No. 88 (A. Poole and F. Gill, Eds.). Philadelphia: The Academy of Natural Sciences; Washington D.C.: The American Ornithologists' Union.

Svensson, L. 1984. Identification guide to European passerines, 3rd ed. Stockholm, Sweden.

U.S. Fish and Wildlife Service and Canadian Wildlife Service. 1978. North American bird banding manual, Vol. 2 (revised 1980). Washington, D.C. and Ottawa, Ontario.

Wald, A., and J. Wolfowitz. 1946. Tolerance limits for a normal distribution. Ann. Math. Stat. 17:208-215.

Weinberg, H. J., and R. R. Roth. 1994. Rectrix shape as an indicator of age in the Wood Thrush. J. Field Ornithol. 65:115-121.

Figure 1. Top panel shows an Image-1 image of a representative HY/SY (a) and AHY/ASY (b) Ovenbird overlaid with a 1.5 mm grid. Middle panel shows line segments x and y and the angles of the segments computed by Image-1. The angle of segment x is 140° and 118° in (c) and (d) respectively. The angle of segment y is 215° and 218° in (c) and (d) respectively. Bottom panel depicts the tip-angle measurements (°) obtained by subtracting the two line segment angles (140° - 215° = 75° tip angle for HY/SY; 218° 118° =100° tip angle for AHY/ASY).

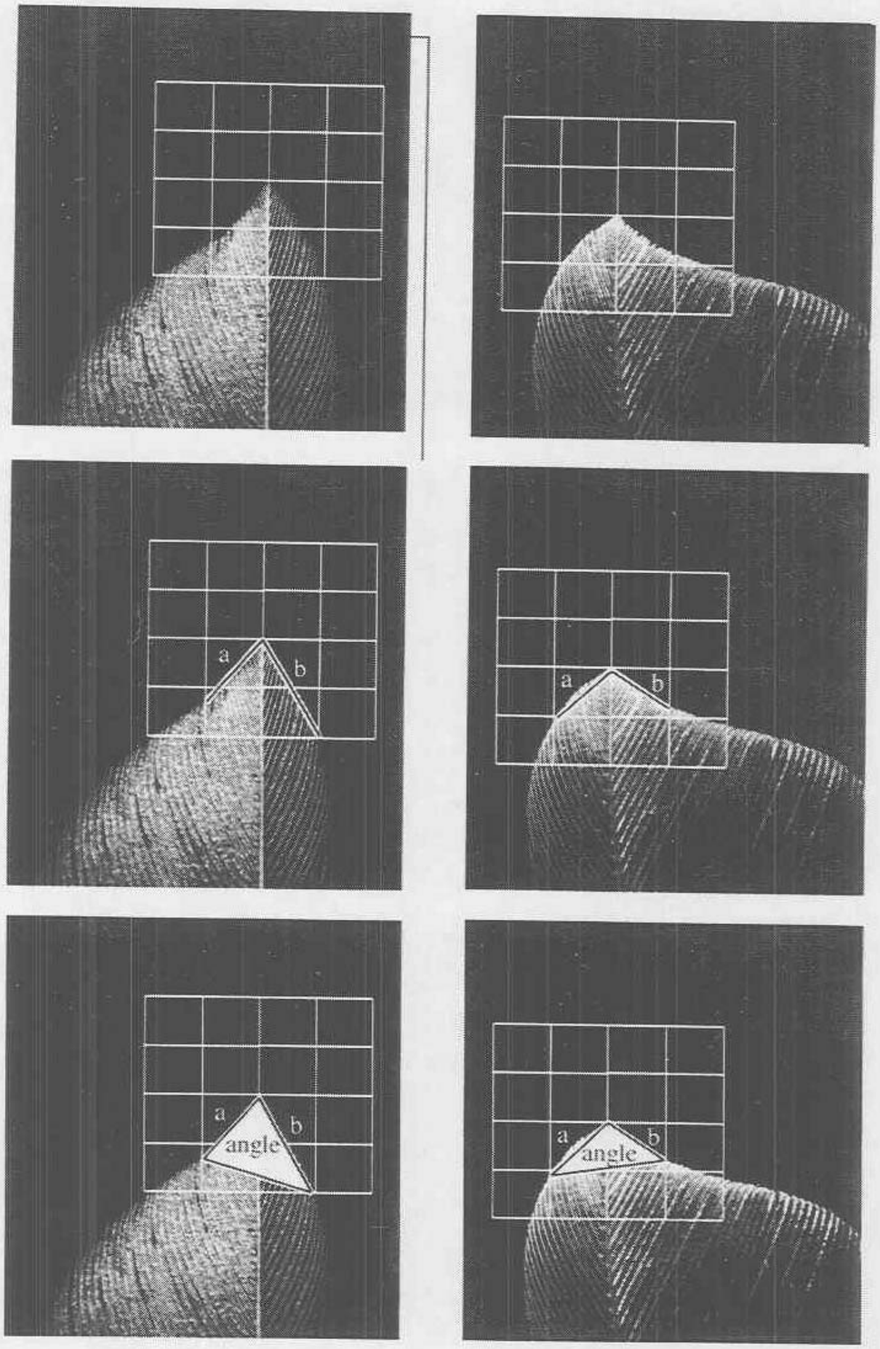
a
b
a
b
a
angle
b
a
angle
b

Figure 2. Mean and standard deviation of Ovenbird rectrix tip angles (°) in 1993 and 1994.

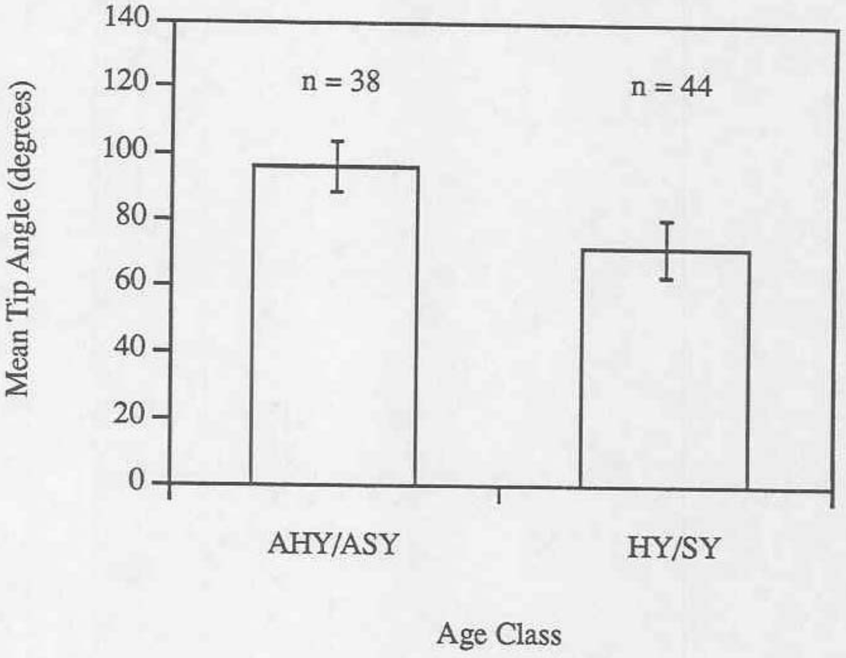
140
120
100
80
60
40
20
0
Mean Tip Angle (degrees)
n = 38
n = 44
AHY/ASY
HY/SY
Age Class

Table 1. Number of Ovenbird rectrices collected from each age-class in each geographic location. The sampling period indicates the time of rectrix collection; stage indicates whether birds were breeding (B), migrating (M), or wintering (W) when feathers were collected.

Site	Sampling Period	Stage	HY/SY	AHY/ASY	Total
Chequamegon National Forest, WI	July 1993	B	5	4	9
St. Croix River, WI/MN	July 1993	B	3	5	8
Bon Secour NWR, Alabama	Sept-Oct 1993	M	20	17	37
Long Point Bird Observatory, Ontario	Sept-Oct. 1993	M	11	5	16
Island Beach, NJ	Sept-Oct. 1993	M	1	2	3
Toronto Bird Observatory, Ontario	Sept-Oct. 1993	M	3	0	3
Manomet Bird Observatory, MA	Sept 1993	M	1	0	1
Guanica National Forest, PR	January 1994	W	0	5	5
Total			44	38	82

CHAPTER IV

EFFECTS OF HABITAT FRAGMENTATION ON DEMOGRAPHY AND RECRUITMENT IN OVENBIRDS

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ABSTRACT

An accurate assessment of how habitat fragmentation affects organisms requires a knowledge of population demography in both fragmented and contiguous habitats. We used late-summer mist-net captures to study the adult age- and sex-structure, return rates, and recruitment of Ovenbirds (Seiurus aurocapillus) in fragmented and contiguous habitats in Wisconsin from 1991-1993. In both habitats, we detected a strong male sex-bias ($P<0.005$ on both fragments and in contiguous habitats). These male-to-female ratios did not differ between habitats. In 1993, the ratio of first-year breeders to experienced breeders did not differ between fragmented and contiguous habitats in a one-year sampling period ($P = 0.590$). Recapture rates between years tended to be higher on fragments than contiguous habitat ($P = 0.077$), but recruitment, based on adult-to-juvenile captures, was greater on contiguous habitat than fragmented habitat ($P = 0.012$). We conclude that recruitment was significantly altered by fragmentation, that fragmentation did not

significantly alter sex ratios on the forests we studied, and suggest that fragmentation may differentially alter the age distribution and site fidelity of males and females.

INTRODUCTION

Habitat fragmentation has become a major issue in recent years, and has been the focus of much research. Literature reviews list literally hundreds of papers dealing with fragmentation and animal populations, most appearing since 1967 (Faaborg et al., in review). For species with low dispersal abilities, decreased population size and increased isolation due to habitat fragmentation can increase the probability of local extinction of species (Gilpin 1987). The effect of fragmentation on highly vagile species is less apparent i because individuals can move among subpopulations and "rescue" subpopulations from ~i local extinction (Brown and Kodric-Brown 1977). However, fragmentation may affect these populations by changing the distribution of age classes and sexes across habitat types (aliens 1976). These factors, in turn, can influence the population growth and the long term persistence of a population (aliens 1976, Kareiva et al. 1993). Understanding the degree to which fragmentation influences the distribution of different kinds of individuals requires comparison of population structure in both fragmented and contiguous habitats.

We studied the demography and recruitment of a forest-nesting Neotropical migrant, the Ovenbird (Seiurus aurocapillus). Ovenbird populations have declined 1% per year from 1978-1989 (Bobbins et al. 1989), and habitat fragmentation has been implicated as one cause of this decline (Porneluzi et al. 1993). Although the mechanisms that reduce Ovenbird reproduction on fragments have been well-documented (Gibbs and Faaborg I 1990, Villard et al. 1993, Donovan et al. manuscript), information is lacking regarding how fragmentation affects the distribution of age classes and sexes across habitat types.

Data are needed to determine of the size of habitats required to maintain the age- and sex distributions found in contiguous habitats and to determine if site-fidelity of individuals to fragments is equal to the site fidelity of contiguous habitats.

We examined these questions by comparing Ovenbird demography and recruitment in fragmented and contiguous habitats using banding (mist netting). Our goals were to: 1) document the recruitment of individuals to breeding populations on fragmented and contiguous forests, 2) determine the age-and sex-structure of adult Ovenbirds on fragmented and contiguous forests, and 3) determine the site fidelity of Ovenbirds to fragmented and contiguous forests. In addition, we discuss the validity of using mist-nets to assess the viability of a population.

STUDY AREAS AND METHODS

We studied Ovenbirds in two study regions: the St. Croix River Valley in Minnesota and Wisconsin, and the Chequamegon National Forest in northwest Wisconsin. The St. Croix study region is 26.5% forested with a mean fragment size of 328.5 ha. By contrast, the Chequamegon study region was 94.8% forested with a mean fragment size of 29,162 ha (Thompson et al., in review). In each region, we studied Ovenbirds on four forested plots from 1991-1993. Ovenbirds occurred on all plots, and their abundance did not differ between fragmented and contiguous plots (Donovan et al. manuscript). In 1991, three plots were studied in each region. In 1992, we added an additional plot in each region. In 1993, three plots were studied in each region, but one plot in each region differed from the 1991 plots (Table 1).

Study plots were approximately 22 hectares in size. All plots in the Chequamegon National Forest were 600m x 300m. The shape of study plots within fragmented habitats of the Saint Croix River Valley depended on forest size and edge but was as rectangular as possible. Plots were located within mature maplebirch-basswood forest (Acer saccharum Betula nigra -Tilia americana), but also had a strong component of Northern red oak (Quercus rubra). Sites appeared to be homogeneous in forest structure (Donovan, unpubl.). The non-forested portion of these landscapes was predominantly cool-season pasture.

In each plot, we randomly selected a 600 m "line" at least 70 m from a habitat/forest ecotonal edge along which birds were sampled in mist nets. A net line consisted of twelve mist nets spaced at 50 m intervals. Each net was 12 m long with a 36 mm mesh size. Netting in the St. Croix and Chequamegan areas was done simultaneously. We began banding when we noticed a significant number of fledglings on a plot (early July), and ended 3 weeks later (late July). We ran the banding line at a plot for two consecutive days, then moved nets to a new plot and sampled there. After all plots within a region were sampled, we repeated the sampling protocol so that the banding line in each plot was operated for four days.

Mist nets were opened 1/2 hour before sunrise and remained open for approximately 6 hours per day, providing 72 net hours per day on each plot (12 nets * 6 hours per day). Nets were monitored for 1728 net hours in 1991, 2304 net hours in 1992, and 1728 net hours in 1993. Because our sampling was standardized across both regions, we present results based on total captures and not as birds per net hour.

We banded every Ovenbird captured, and recorded its capture location, time of capture, age, sex, wing chord, and weight. We identified breeding females based on a brood patch and breeding males based on a cloacal protuberance (Pyle et al. 1987). Birds were aged as adults or juveniles based on plumage characteristics (Pyle et al. 1987).

In 1993 only, we collected the fourth rectrix of each breeding adult and analyzed rectrix shape. For each rectrix, we measured the angle of the feather tip on a 1.5 mm grid. We classed birds as older breeders (birds that lived through at least one previous breeding season, classified as After Second Year (ASY) birds by the Bird Banding Lab) or inexperienced breeders (birds that are attempting to breed for the first time, also termed Second Year (SY) birds). These age-classifications for 1993 were based on tip-angle discriminant functions described by Donovan and Stanley (in press). In general, adults with tapered rectrices were classified as first year breeders (SY birds), and adults with paddle shaped rectrices were classified as experienced breeders (ASY). Previously banded birds were scored as recaptures, and birds recaptured within the same year were recorded as a single capture.

Statistical Analyses

All analyses focused on differences in the dependent variable between fragmented and contiguous forests. We determined if adult-to-juvenile ratios, sex ratios, age ratios, and return rates of ovenbirds differed on fragmented and contiguous forests using Chi Square Test for Independence. We used a Goodness of Fit test to determine if sex ratios in each landscape deviated from 1 to 1 and used Fisher's Exact Test to determine if the age distribution of males and females differed on fragmented and contiguous forests.

For all tests, we computed the probability of a Type II error and statistical power using the NCSS-Power Analysis and Sample Size program (Hintze 1991). We computed the effect size, w, for a given Chi-Square as: $X2 = N w2$, where N is the total sample size. We used the calculated effect size, total sample size, and a Type I error rate = 0.05 to significant or non-significant based on the Type I and II error rates.

RESULTS

Recruitment

Adult to juvenile ratios were significantly different on contiguous and fragmented forests (Chi-Square = 6.239; P = 0.012; Power = 0.70; Table 2). On contiguous forests, for every juvenile captured, 2.09 adults were captured. On fragments, for every juvenile captured, 4.52 adults were captured (Table 2).

Sex Ratios

The sex ratio was male-biased on both fragments (Chi-Square = 15.92; P < 0.005 ; Power = 0.97) and contiguous forests (Chi-Square = 7.92; P < 0.005 ; Power = 0.80). The ratio of females to males did not differ significantly between fragmented and contiguous forests (Chi-Square = 0.975; P = 0.324; Power = 0.17; Table 2). The female-to-male ratio was 1:1.9 on contiguous forests (34.8:65.2) and 1:2.6 on fragments (27.9:72.1; Table 2).

Age Ratios

The 1993 age structure of breeding adult Ovenbirds (males and females combined) on fragmented and contiguous forests did not differ (Chi-Square = 0.290; P = 0.59; Table 2). We detected trends when age structure was analyzed separately by sex, but these trends were not statistically significant (Table 3); the age structure of breeding males and females did not differ between fragmented and contiguous sites (Chi Square = 2.121; P = 0.145; Power = 0:07 and Chi Square = 1.637; P = 0.201; Power = 0.07, respectively). On fragments, 8 ASY (older) and 2 SY (young) adult males were captured, whereas 6 ASY and 6 SY adult males were captured in contiguous habitat (Table 3). On fragments, 2 SY and 1 ASY adult females were captured, whereas 2 SY and 6 ASY adult females were captured in contiguous habitat (Table 3).

Site Fidelity

The number of adults captured in one year and re-captured in another tended to differ between fragmented and contiguous sites (Chi-Square = 3.134; P = 0.077; Power = 0.42; Table 2). Of 54 and 63 birds banded on fragmented and contiguous forests respectively, 9 were recaptured on fragments and 4 were recaptured on contiguous forests. On fragments, for every 5 birds banded, one was recaptured. On contiguous forests, for every 15 birds banded, one was recaptured (Table 2). All of the recaptured birds on contiguous forests were males, while seven of nine recaptured birds on fragments were males.

DISCUSSION

Recruitment

Our results show that recruitment was lower in fragmented habitat than contiguous habitat. With lower recruitment in fragments and in the absence of immigration, population growth on fragments is expected to be lower than population growth in contiguous habitats. It is possible, however, that populations on fragments are being subsidized by receiving immigrants produced elsewhere. If so, these sites are suitable for investigating how fragmentation affects the age and sex distribution in widely dispersing species.

Results from this banding study are in accord with results from detailed observations of nests on the same plots (Donovan et al. manuscript). Banding results indicate that for every juvenile captured, 2.09 adults were captured on contiguous forests (juvenile to adult ratio = 0.48), whereas for every juvenile captured, 4.52 adults were captured on fragments (juvenile to adult ratio = 0.22, Table 2). These ratios closely match the probability that a nest would survive to fledging. Ovenbird nesting success was 43% in contiguous forests and was 20% in fragmented habitats.

Although the sample is small, the use of mist nets may be a useful technique to document general patterns of recruitment for ground-nesting and ground-feeding species such as the Ovenbird. The usefulness of this technique, however, depends upon local population size and undoubtedly varies from region to region. In habitats or regions where population size is low, capture rates may be very low, and mist-netting may not be a cost effective method of measuring recruitment (Faaborg and Clawson, unpubl. data).

Sex Ratios

We detected a male sex-bias in both fragmented and contiguous habitats, but the biases were not significantly different from each other. Other studies of Ovenbird sex ratios documented that male sex-bias is common on small fragments (Gibbs and Faaborg 1990), but this pattern varies depending on geographic location of the study (Villard et al. 1993). In the center of the breeding range where population densities are high, the sex ratio is closer to 1:1 on fragments than on fragments at the edge of the range (Villard et al. 1993). Our study areas were located near the center of the Ovenbird's breeding range, where population densities are quite high relative to other areas (Van Horn and Donovan, 1994). If density-dependent habitat selection is operating in both males and females, and if both males and females perceive a diminished quality of high-density contiguous forests and can move in response to it, both males and females may disperse into the sub-optimal fragments (Fretwell and Lucas 1970), equalizing the distribution of the sexes across habitat types.

Adult male-sex bias is common in most monogamous passerine species (reviewed in Breitwisch 1989), even in unfragmented habitats. Wander (1985) documented that only 67% of banded male Ovenbirds in a >10,000 ha. Pennsylvania forest were paired. Similarly, 75% of male Ovenbirds were paired in 18,000 km2 Missouri Ozarks (Porneluzi, unpubl). Our results demonstrate that, in the center of Ovenbird breeding distribution, sex-ratios are maintained on fragments that averaged 320 ha. Although the sex ratios did not differ between fragmented and contiguous forests, recruitment did differ, suggesting that mechanisms other that unpaired individuals were responsible for decreased recruitment on the fragments (see also Donovan et al. manuscript).

Age Ratios and Site Fidelity

Based on a one year sampling snapshot, we did not detect differences in age structure (males and females together) between fragmented and contiguous forests. However, our results suggest that fragmentation may alter the age-class distribution differently for males and females, with fragments dominated by older males and younger females and contiguous forests dominated by younger males and older females. Although these one-year patterns of age and sex distribution on fragmented and unfragmented forests are non-significant ($P>0.15$), the statistical power of these tests is exceptionally low. If differences did truly exist, we had <10% probability of detecting them.

However, there are good biological reasons that suggest why the age-distribution of males and females may differ between habitat types. Fragments should be dominated by inexperienced female breeders for two reasons. First, females have been suggested to have a greater natal dispersal than males (Greenwood and Harvey 1982), and in a given year fragments may have more "openings" for dispersers because of higher predation pressures on adult females in fragments than contiguous habitats. Second, female Ovenbirds on fragments may have higher breeding dispersal than females on contiguous habitats, because experienced females that bred on fragments in the previous year were more likely to have failed nest attempts and would subsequently disperse to new areas (Martin and Li 1992). By contrast, females that nest in contiguous habitats have a greater probability of fledging young. Successful females are more likely to be site-faithful (Martin and Li 1992), and in turn, populations on contiguous habitats would show an older age-structure compared to populations on fragments.

Male passerines, by contrast, exhibit more site fidelity than females (Greenwood and Harvey 1982), and their probability of returning to an area is not as dependent on previous year's nesting success. Most of our recaptures (11/13) were males, indicating that males have a higher site attachment than females in both habitats, and these recaptures were greater on fragments than contiguous habitats. Wander (1985) reported that 5/16 (31%) of Ovenbirds returned to a >10,000 ha. forest, while 3/8 (38%) returned to small fragments, and most of the returning birds (87.5%) were males. It appears from this study and others that adult male Ovenbirds on fragments are site-faithful from year to year, even if they never find a mate (Wander 1985, Hawk Mountain Sanctuary unpubl. data, Porneluzi, unpubl. data). Either the rewards of being site faithful (knowledge of the habitat and predators) offset the cost of dispersing, or the cost of dispersing is too great in fragmented habitats. In contiguous habitats, even a very short-distance dispersal (> 100m) by male Ovenbirds may have resulted in our inability to capture it. Color-banding studies may elucidate these differences.

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LITERATURE CITED

Breitwisch, R. 1989. Mortality patterns, sex ratios, and parental investment in monogamous birds. Curr. Ornithol. 6:1-50.

Brown, J. H., and A. Kodric-Brown. 1977. Turnover rates in insular biogeography: effect of immigration and extinction. Ecology 58:445-449.

Donovan, T., and C. M. Stanley. In press. A new method of determining Ovenbird age based on rectrix shape. J. Field Ornithol.

Faaborg, J., M. Brittingham, T. Donovan, and J. Blake. In review. Neotropical migrant responses to habitat fragmentation in the temperate zone. In Ecology and management of Neotropical migratory birds: A synthesis and review of the critical issues (D. Finch and T. Martin, eds.). Oxford University Press.

Fretwell, S. D., and H. L. Lucas. 1970. On territorial behavior and other factors influencing habitat distribution in birds. Acta Biotheoretica 19:16-36.

Gibbs, J. P.; and J. Faaborg. 1990. Estimating the viability of Ovenbird and Kentucky Warbler populations in forest fragments. Conserv. Biol. 4:193-196.

Gilpin, M. E. 1987. Spatial structure and population viability. In Viable populations for conservation (M. E. Soule, ed.). Cambridge University Press, Cambridge.

Greenwood, P. J., and P. H. Harvey. 1982. The natal and breeding dispersal of birds. Ann. Rev. Ecol. Syst. 13:1-21.

Kareiva, P., J. Kingsolver, and R. Huey. 1993. Biotic interactions and global change. Sinauer Associates Inc., Massachusetts.

Martin, T. E., and P. Li. 1992. Life history traits of open- versus cavity-nesting birds. Ecology 73:579-592.

Porneluzi, P., J. C. Bednarz, L. Goodrich, N. Zawada, and J. Hoover. 1993. Reproductive performance of territorial Ovenbirds occupying forest fragments and a contiguous forest in Pennsylvania. Conserv. Biol. 7:618-622.

Pyle, P., S. N. G. Howell, R. P. Yunick, and D. F. DeSante. 1987. Identification guide to North American passerines. Slate Creek Press, Bolinas, California.

Robbins, C. S., J. R. Sauer, R. Greenberg, and S. Droege. 1989. Population declines in North American birds that migrate to the Neotropics. Proc. Natl. Acad. Sci. 86.

Villard, M. A., P. R. Martin, and C. G. Drummond. 1993. Habitat fragmentation and pairing success in the Ovenbird (Seiurus aurocapillus). Auk 110:759-768.

Van Horn, M., and T. M. Donovan. 1994. Ovenbird (Seiurus aurocapillus). In The Birds of North America, No. 88 (A. Poole and F. Gill, Eds.). Philadelphia: The Academy of Natural Sciences; Washington D.C.: The American Ornithologists' Union.

Wander, S. A. 1985. Comparative breeding biology of the Ovenbird in large vs. fragmented forests: Implications for the conservation of Neotropical migrant birds. Ph.D. Dissertation, Rutgers Univ., New Jersey.

Wiens, J. 1976. Population responses to patchy environments. Ann. Rev. Ecol. Syst. 7:81-120.

Table 1. Number of Ovenbirds captured per site in fragmented and contiguous landscapes in Wisconsin. Habitat statistics for each site are based on average landscape statistics within 10 km of the site.

Landscape	Site	UTM East, North	% Forest Area (10 km)	Mean Patch Size (ha)	Edge Index (m/ha)	Years Sampled	Total Captures
Fragmented	O'Brien	5008325, 516495	23.67	181.7	8.7	91,92,93	29
Fragmented	Interstate	5026320, 529435	24.94	280.4	8.0	91,92,93	11
Fragmented	Wild Mtn.	5036810, 522150	25.26	379.5	7.4	91,92	25
Fragmented	Wild River	5040990, 520700	33.20	454.4	7.0	92,93	40
Contiguous	Town Hall	5116110, 648010	90.93	28575.0	4.2	91,92	6
Contiguous	Drummond	5130600, 628780	94.59	29725.0	3.1	91,92,93	43
Contiguous	HW - East	5130900, 652880	92.92	29200.0	3.6	91,92,93	57
Contiguous	HW - West	5131050, 652220	92.76	29150.0	3.8	92,93	39

Table 2. Number of birds captured in mist nests and results of Chi-Square analyses comparing Ovenbird population characteristics in fragmented and contiguous forests in Wisconsin. Capture percentages are given in parentheses.

Dependent Variable (DV)	Levels of D.V.	Fragmented	Unfragmented	Chi-Square	P	Power	Significant Difference?
Sex	Male	62 (72.09)	60 (65.22)	0.975	0.324	0.167	No
	Female	24 (27.91)	32 (34.78)				
Adult Age	Inexperienced (SY)	4 (30.77)	8 (40.00)	0.290	0.590	0.120	No
	Experienced (ASY)	9 (69.23)	12 (60.00)				
Productivity	Juvenile (HY)	19 (18.10)	44 (32.35)	6.239	0.012	0.705	Yes
	Adult (AHY)	86 (81.90)	92 (67.65)				
Return Rate	Recaptured	9 (16.67)	4 (6.35)	3.134	0.077	0.425	Yes
	Not Recaptured	45 (83.33)	59 (93.65)				

Table 3. Number of birds captured in mist nests and results of Chi-Square analyses comparing the age and sex distributions of breeding adult Ovenbirds in fragmented and contiguous habitats in Wisconsin in 1993. Capture percentages are given in parentheses.

Sex	Age	Fragmented	Contiguous	Chi-Square	P	Power	Significant Difference?
Males	Inexperienced (SY)	2 (20.00)	6 (50.00)	2.121	0.145	0.0668	N.S. Trend
	Experienced (ASY)	8 (80.00)	6 (50.00)				
Females	Inexperienced (SY)	2 (66.67)	2 (25.00)	1.637	0.201	0.0733	N.S. Trend
	Experienced (ASY)	1 (33.33)	6 (75.00)				

CHAPTER V

DEMOGRAPHY OF MIGRATORY BIRDS IN HABITAT SOURCES AND SINKS

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ABSTRACT

Fragmentation of breeding habitat in North America has been implicated in the decline of forest-nesting Neotropical migrant birds. Yet, direct evidence to support or refute the fragmentation hypothesis is weak or lacking, and direct measures of reproductive success in both fragmented and unfragmented habitats are needed. We used a comparative approach to test the fragmentation hypothesis in three forest-nesting migrants: Ovenbird (Seiurus aurora aurocapillus), Red-eyed Vireo (Vireo olivaceus), and Wood Thrush (Hylocichla mustelina). We surveyed birds and monitored reproductive success on 28 study plots in fragmented and contiguous forests in two geographic regions within the Midwestern United States. Support of the fragmentation hypothesis required that reproductive success

was reduced on fragments m both regions, although the mechanism by which this reduction occurred varied regionally.

In both regions, distribution of individuals was not negatively altered by fragmentation, but total nest failure was significantly higher on fragments than contiguous forests (P = 0.053). This increase in total nest failure was attributed to increased nest predation (P = 0.093) and increased brood parasitism by the Brown-headed Cowbird (Molothrus ater. P = 0.009). In addition to increased total nest failure, partial nest failure due to Cowbird parasitism led to a reduction in the number of host fledglings. Although the factors that result in lower recruitment appeared to be species-specific, total nest failure and partial nest failure acted in concert to reduce the number of offspring per adult on fragments for all three species.

We used simple population growth models to assess the viability of the three species in fragmented and contiguous habitats in both regions. In general, populations on fragments appeared to be population sinks and populations on contiguous forests appeared to be population sources. Projected growth indicated that in the absence of immigration, Ovenbird and Red-eyed Vireo populations should go extinct on fragments in both regions, while Wood Thrush populations should maintain themselves at equilibrium or slightly decline on fragments. By contrast, Wood Thrush and Red-eyed Vireo populations should increase dramatically in contiguous habitats in both regions in the absence of emigration, and Ovenbird populations would maintain themselves at equilibrium in one region and increase in the other.

We suggest that habitat fragmentation reduces reproduction on a local scale and has ramifications for the population at spatial scales beyond the local scale. Thus, a clear understanding of population demography depends on examination of demographic dynamics within and among sources and sinks. We emphasize that the long-term viability of these species depends on maintaining large tracts of forest throughout the breeding range until the spatial scale at which source and sink populations interact can be determined

INTRODUCTION

Many species of Neotropical migrant songbirds have undergone significant population declines since 1966 (Robbins et al. 1989). Three non-exclusive hypotheses may explain these declines (Askins et al. 1990, Wilcove and Robinson 1990, Finch 1991, Martin 1992, Faaborg et al. in review, and Sherry and Holmes 1993): 1) migrant passeriformes may experience increased mortality as they migrate between their wintering grounds in the Caribbean, Mexico, and Central America and their breeding grounds in North America; 2) migrant passeriformes may experience increased mortality on their wintering grounds due to anthropogenic changes m habitat (e.g., tropical deforestation); and 3) migrant passeriformes may experience reduced fecundity (number of offspring produced per year) and/or fitness (survival of offspring to reproduction) on the breeding grounds due to anthropogenic habitat fragmentation and loss.

The habitat fragmentation hypothesis provides a framework for predicting charges in bird distribution or reproductive success based on local habitat and landscape patterns (Harris 1984). Support of the fragmentation hypothesis requires that 1) fragmentation affects the distribution of species across habitats/landscapes, and this shift in distribution results in population decline on either local, regional, or range-wide scales; or 2) fragmentation decreases productivity and/or survivorship of birds that nest in fragmented habitats/landscapes, and this reproductive/survivorship dysfunction results in population decline on either local, regional, or range-wide scales.

Fragmentation is expected to negatively influence those species that historically have inhabited large contiguous tracts of habitat with a relatively low density of edge (Temple and Cary 1988). The reduction in reproductive success in the Midwestern United States is often related to the degree of fragmentation and the amount of edge within a landscape (Robinson et al. manuscript). In small, fragmented habitats, birds experience increased nest predation (Hoover et al. in press, Paton 1994), increased brood parasitism by the Brownheaded Cowbird (Molothrus fir, reviewed by Robinson et al. 1993), and decreased pairing success (Gibbs and Faaborg 1990, Villard et al. 1993, Van Horn et al. 1994). Together, these mechanisms may limit the reproductive success of forest-nesting migrants (Faaborg et al., in review) and may result in lower recruitment of individuals into the breeding population. This lower recruitment may negatively influence future demographic trends at the local scale (Sherry and Holmes 1992), and may explain why most long-term declines of forest-nesting migrants appear in fragmented habitats (Askins et al. 1990).

Population Viability

To adequately assess the effects of fragmentation and the size of habitats needed to maintain populations, one must consider the “area in which young can be produced in sufficient numbers to replace adult attrition under the poorest conditions" (Bobbins 1979). If reproduction does not compensate for adult mortality, then local populations are sinks: they will either go extinct or will be maintained via constant immigration from birds produced elsewhere (Brown and Kodric-Brown 1977, Pulliam 1988). Alternatively, if reproduction equals or exceeds adult mortality, then local populations are sources: they will sustain themselves or export excess individuals to other areas (Pulliam 1988).

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Many studies have used indirect methods to assess population viability. Indirect methods include utilizing artificial nests (reviewed by Paton 1994), documenting presence/absence of young produced on habitats of varying size (e.g., Porneluzi et al. 1993), and documenting the ratio of juveniles to adults on forests of varying size (e.g., Bollinger and Linder 1994, Donovan and Faaborg, manuscript). However, such indirect methods are insufficient to uncover the causal mechanisms of reproductive dysfunction that ultimately limit populations on fragmented and unfragmented forests.

Because habitat features may alter the demography of a population by directly affecting reproduction and survival, <u>direct</u> examination of fitness components in relation to habitat patterns at local sites and across regions is needed (Martin 1992). Direct measurement of reproductive success is necessary to compare the average number of offspring per adult on both fragmented and contiguous habitats and evaluate whether populations are able to maintain themselves (Pulliam 1988). A few exceptional studies have directly examined species-specific characteristics of reproductive success of forest birds in either fragmented (e.g., Gibbs and Faaborg 1990, Villard et al. 1993, Robinson 1992, Roth and Johnson 1993) or contiguous habitats (e.g., Holmes and Sherry 1992); even fewer have examined these characteristics in both fragmented and contiguous landscapes (Hoover et al., in press). Yet, this knowledge is required to test the fragmentation hypothesis and to manage viable populations (Martin 1992).

We tested whether fragmentation affects the distribution, reproduction, and viability of three forest nesting Neotropical migratory bird species in two geographic regions in the Midwestern United States. Our objectives were to: 1) document the distribution and abundance of forest-breeding Neotropical migrant birds in fragmented and contiguous forests in two geographic locations; 2) document the reproductive success and factors that limited reproductive success of forest-breeding Neotropical migrant birds in fragmented and contiguous forests in these two geographic locations; and 3) assess the population viability by using simple population growth models for bird populations on fragmented and contiguous forests in the two geographic locations.

STUDY SPECIES

We studied three forest-nesting Neotropical migrant songbirds, the Ovenbird (Seiurus aurocapillus), Red-eyed Vireo (Vireo tolivaceus), and Wood Thrush (Hylocichla mustelina). All three species breed in midwestern and eastern deciduous forests in the United States. Breeding Bird Survey (BBS) data from 1966 to 1992 indicate that the Wood Thrush has undergone a significant, range-wide decline, the Red-eyed Vireo has undergone a significant, range-wide increase, and the Ovenbird has undergone a nonsignificant range-wide increase (Peterjohn and Sauer 1994). BBS trends in the Midwest, where our study areas were located, reflect range-wide trends (Thompson et al. 1993). As yet, it is not clear whether the differential changes in population trends are related to differential responses to habitat fragmentation or to other causes.

STUDY AREAS

We studied Ovenbird, Red-eyed Vireo, and Wood Thrush distribution and reproductive success in Missouri (MO) and Wisconsin/Minnesota (WI/MN), in 1991-1993 (Table 1). We selected these regions because they coincide with the center (WI/MN) and southwestern edge (MO) of the Ovenbird's breeding range. WINN represents the northwestern edge of the Wood Thrush breeding range whereas MO represents the western-center of its breeding range. The Red-eyed Vireo has a broad breeding distribution and both the MO and WI/MN regions are west-centrally located.

Within each region, we examined bird demography on forest fragments in an agricultural landscape and on unfragmented (contiguous) forests. For clarity, we refer to each landscape (fragmented or contiguous) and region (MO or WI/MN) combination as a study area (n = 4). We studied 6 to 9 forest plots in each study area and treated these plots as replicates in analyses. In Missouri, 9 fragmented study plots were situated in central Missouri, and 8 contiguous study plots were situated within the heavily forested Ozarks in southeast Missouri. In Wisconsin/Minnesota, 6 fragmented study plots were situated in the lower St. Croix River Valley, and 6 contiguous study plots were situated within the heavily forested Chequamegan National Forest (WI). We studied all WI/MN plots in 1991 and 1992. In Missouri, we studied 9 fragmented plots and 6 contiguous forest plots in 1991. In 1992, we studied 8 plots within fragmented and 8 plots within contiguous forests. In 1993, we located and monitored nests on a subset of plots in each study area to increase the nest sample size.

All study plots were approximately 22 ha in size. Because our primary objective was to measure reproductive success in fragments and contiguous forests, we located our plots in fragments large enough to insure that area-sensitive species would be present and that populations would consist of both males and females (Table 1). We considered a forest tract a fragment based on several criteria: size (ha), edge density (m of edge per ha), and percent core area (percentage of forest > 250 m from edge). Thus, although fragment size ranged from 181 km^2 to 1872 ^{2,} all fragments had similar edge density and percent core areas (Table 1). The contiguous forests in WI and MO averaged 29,150 km^2 and 26,769 km^2, respectively (Table 1).

We located study plots within relatively mature (> 40 years) oak-hickory forest in MO and maple-basswood-birch forest in WI/MN. We selected WINN plots with a strong component of oak (Quercus rubra) to minimize heterogeneity of tree genera among sites. Despite differences in forest composition, all forests appeared to be homogeneous in structure (Donovan, unpubl.). In both regions, the non-forested portion of fragmented landscapes was predominantly cool-season pasture and row crops.

METHODS

Distribution and Abundance

We surveyed bird abundance at points located on a 150 m grid. Grids were established by randomly selecting a point within the forest and subsequently situating a grid around the random point. We surveyed 15 points at grid intersections that were located >70 m from a habitat/forest ecotonal edge because we were interested in sampling forest species, not edge species.

We visited each point four times on each plot during the breeding season and counted forest-nesting Neotropical migrants and Brown-headed Cowbirds during a ten minute count (Verner 1988). Three to four different observers conducted surveys at each point in each year to minimize observer variability (Verner 1989). Surveys began after territories were established and ended when most nests had fledged (May 5 - June 15 in MO; May 28 -July 2 in WI/MN).

In each ten minute count, we recorded bird defections within 50- and 70-meter fixed radius circles, as well as total (unlimited distance) defections. We computed the mean number of defections in each distance class for each plot in each year. Plot means were based on 15 counting points that were censused four times within a season (n = 60 ten minute counts). In this paper, we use the unlimited distance class in analyses to maximize detections and ensure that territorial birds near edges were adequately sampled. Although the distribution patterns were similar for all three distance classes, we also present results based on within-50m and within-70m radii for between-study comparisons.

We compared bird abundance on fragmented and contiguous forests using a repeated measures analysis of variance, with landscape (fragmented or contiguous) and region (MO or WI/MN) as main effects and year as a repeated effect. Sites within a landscape were used as the error term. We used a Type I error rate = 0.1 for all analyses to reduce the probability of committing a Type II error, i.e, concluding that effects are not different when they actually were.

Reproductive Success and Factors Limiting Reproduction

We located and monitored nests on a subset of the study plots in 1991-1993 to assess reproductive failure and cause-specific mortality in fragmented and contiguous forests in both regions (Table 1). Nests that were located when active and were low enough (<14 m height) to be monitored by direct observation were included in analyses. All active Ovenbird and Wood Thrush nests were included in analyses, but canopy-nesting Red-eyed Vireos were excluded in analyses. In total, we monitored 135 Ovenbird nests, 62 Red-eyed Vireo nests, and 119 Wood Thrush nests. For each nest, we recorded the number of host and cowbird eggs, chicks, and fledglings every 3-5 days. We recorded each nest's fate as successful (nests that fledged at least one host species young) or failed (nests that fledged no host species young). We classified failed nests as depredated (nests in which nest, eggs, or young nestlings disappeared), abandoned (eggs or nestlings left unattended in nest), failed due to stochastic events (weather or other random events, such as inadvertent trampling on a nest), or failed due to cowbird parasitism (no host young fledged due to cowbird parasitism, although cowbirds may have fledged successfully). Because many parasitized nests were successful in that they fledged both cowbird and host young, we distinguished between the proportion of nests that failed due to cowbird parasitism (parasitism failure) and the proportion of nests containing cowbird eggs or young (Parasitism rate).

Daily Mortality and Nesting Success

We calculated nesting success on a per nest basis using the Mayfield (1975) method. These estimates consider all nest failures, irrespective of cause. We considered the first observation day as the first day of egg-laying (if the nest was located before the first egg was laid) or the day the nest was located (if the nest was located after the first egg was laid). We observed nests until fledging or failure occurred For each species, we computed daily mortality as the total number of failures divided by the total number of observation days pooled across all nests within each study area. We calculated daily survival for each species in each region as (1- daily mortality). We assumed that daily survival was constant throughout the nest cycle (hayfield 1975), and calculated nesting success as the daily survival rate raised to the exponent which reflects the length of the nesting cycle (as summarized by Ehrlich et al. 1988). This estimate gives the probability that a nest will survive its entire cycle and successfully fledge at least one nestling. We calculated nest failure as (1nesting success). A potential bias occurs if the mean clutch size and duration of the nesting cycle varies between fragments and contiguous forests and between WI/MN and MO. We were not able to determine the exact length of the nesting I cycle because we did not monitor nests daily. However, we do not believe that our estimates of nesting success are biased because the data used by Ehrlich et al. (1988) represent the mean clutch and nest cycle duration across many studies.

For each species, we tested whether daily mortality differed among the four study areas using a Chi-Square analysis with multiple comparisons (Nines and Sauer, manuscript, described in Sauer and Williams 1989). We performed two additional comparisons for each to directly test the research questions of interest: daily mortality on fragments versus contiguous forests and daily mortality in MO versus WI. We used a Type I error rate = 0.1 for all analyses to reduce the probability of committing a Type II error, Le, concluding that effects are not different when they actually are.

Cause-Specific Daily Mortality

To determine the mechanisms that limit reproductive success in fragmented and contiguous forests, we partitioned the total daily mortality (due to any cause) into cause-specific components. For example, to determine how nest predation influenced daily mortality, we summed the total number of nest failures due to predation and divided that number by the total number of observation days to obtain a daily mortality rate due solely to nest predation. In the same manner, we summed the incidences of nest failures due to abandonment, stochastic events, and parasitism, and calculated cause-specific daily mortality estimates for each of the four study areas. For each species, we tested if cause-specific daily mortality differed among the four populations, among fragmented and contiguous forests, and among regions using a Chi-Square analysis with multiple comparisons (Nines and Sauer, manuscript). We considered P values $\leq$ 0.10 significant for these analyses.

Generalized Patterns of Daily Survival and Nesting Success

Our primary research objective was to test whether fragmentation negatively affected the reproduction and viability of Neotropical migrant birds, and whether these effects varied regionally. As noted above, we tested the same hypotheses for each of the three forest-nesting Neotropical migratory birds. Because these separate tests have relatively low statistical power (see below), we used a Combined Probabilities Test (Sokal and Rohlf 1981) to test whether the general patterns of daily mortality differed across landscapes and regions. This test utilizes a series of separate significance tests on different sets of data that test the same scientific hypothesis. Although the tests on the individual species provide a P-value that may or may not be statistically significant, the combined probabilities from separate tests of significance may illuminate a generalized pattern that would not be statistically detected by separate analyses (Sokal and Rohlf 1981). As such, we tested if daily mortality and. cause-specific mortality of Neotropical migrants (Ovenbird, i Wood Thrush, and Red-eyed Vireo combined) differed among landscapes and regions, and considered P-values ≤ 0.10 significant for these analyses.

Effects of Cowbird Parasitism

The Mayfield estimates of daily survival do not account for partial nest losses, i.e., a nest fledging one young is scored the same as a nest fledging four young (both are scored as successful). Yet, partial nest loss may affect Neotropical migrant populations by reducing the number of nestlings per nest Because cowbirds often remove host eggs in nests they parasitize (Lowther 1993), the mean number of host fledglings may differ between successful nests that are parasitized and successful nests that are not parasitized.

We calculated parasitism rates of each species in all four study regions as the percentage of nests containing cowbird eggs and young. For nests that successfully fledged host young, we compared the mean number of fledglings per parasitized nest to the mean number of fledglings in non-parasitized nests using a t-test for each species.

Source-Sink Assessment

Given current reproduction, we sought to determine whether each of the four populations studied could maintain itself without emigration or immigration. We used three demographic components to assess population source-sink status: the mean number of female offspring produced per adult female per year in a population, the probability that those offspring will survive to reproduce, and the survival rate of adults (Pulliam 1988). The first two components determine the recruitment of young into the breeding population. If recruitment of young into the breeding population does not compensate for adult mortality (= 1 -adult survivorship), then the population is a sink. Alternatively, if recruitment of young into the breeding population exceeds adult mortality, then the population is potentially a source, where excess individuals may emigrate to other areas (Pulliam 1988). If:

(1- adult survivorship) = (mean number of female offspring/female/year)* (juvenile survival),

then the population will replace itself (Ricklefs 1973). We directly calculated the mean number of female offspring per female per year from our data, and used estimates of adult survival and juvenile survival from the literature (see below). If (1- adult survival) divided by juvenile survival was greater than the number of observed female offspring per female, we concluded the population was a sink. Conversely, if (1 -adult survival) divided by juvenile survival was less than the number of observed female offspring per female, we concluded the population was a potential source.

To determine whether the four populations studied were sources or sinks, we made the following assumptions regarding the total number of fledglings produced per year, the survivorship of young to the age at first breeding, and the subsequent survival of the adults throughout their lifetime (Ricklefs 1973). First, because all three species studied do not show age-related (first-time breeders versus older breeders) differences in plumage, we could not assess if fecundity per year of first time breeders differed from older breeders; we assumed equal fecundity for all adult age classes. Second, we assumed that Ovenbirds could fledge only one brood per year during our study, whereas we assumed Red-eyed Vireos and Wood Thrushes could fledge two broods per year (Martin, in press). For each species, we calculated the mean number of fledglings per nest in each study area, and divided that number by two to obtain the mean number of female fledglings per nest (the fecundity of females per year). This value was converted to the total female offspring per adult female per year by multiplying by 1 for the single-brooded Ovenbird and by 2 for the double-brooded Wood Thrush and Red-eyed Vireo.

We assumed that all juveniles of all species had a 0.31 probability of surviving to the following breeding season (Greenberg 1980). Although direct estimates of this probability are lacking (because juvenile birds disperse widely, Greenwood and Harvey 1982), juvenile survivorship rates can be indirectly estimated based on data for adult mortality and female productivity (Ricklefs 1973). Greenberg (1980) and Temple and Cary (1988) hypothesized that juvenile survival was 0.31, or approximately 50 percent of adult survival, based on calculations of adult survival and fecundity. This value has been used by other investigators that modeled population dynamics of forest interior birds (Temple and Cary 1988, Thompson 1993, and Howe et al. 1991). Because our goal in assessing source-sink status was to make relative, not absolute, comparisons of the populations in the four study areas, the 0.31 estimate was adequate to address our goal.

We obtained species-specific adult survival estimates (the probability that an adult will survive from one breeding season to the next) from several sources in the literature.

We used each species-specific survival estimate to assess source-sink status in each study region. We used the mean of the species-specific published estimates of adult survival in our population models (below). Although these survival estimates varied from study to study, they were adequate to make relative comparisons of population growth in our four study populations.

Population Projection Models

Source-sink status does not completely describe the population demography of a species because it does not indicate the relative differences in reproduction and how population numbers will change over time. We used the following two-stage population projection model to assess change in population size over time given current reproduction with no immigration or emigration:

$$N_{(t+1)} = (N_{At} * S_{At} + (N_{At} * F_t * S_{Jt}),$$

where t = year of simulation, N = number of adult breeding females, N_{At} is the number of breeding adult females in year t, S_{At} is the survival of breeding female adults from year t to year t + 1, Ft is the mean number of female offspring per adult female in year t, and S_{Jt} is the survival of juvenile offspring in year t to breeding in year t + 1. For each species, we used the mean number of birds censused per ten minute count * 1000 as a starting population size and projected population growth or decline over a twenty year period Our point count estimates provide a reasonable, relative population size of adult females for each of the four study areas. Although singing males axe predominantly counted with point counts, mist netting data indicate that the sex ratios on fragments and contiguous forests in WI and MO did not differ significantly (Donovan, unpubl. and Porneluzi, unpubl., respectively). For the population growth models, we used the average of the published adult survival estimate for each species. Annual adult survival averaged 0.62, 0.56, and 0.67 for Ovenbirds, Red-eyed Vireos, and Wood Thrushes, respectively. We used a value of 0.31 for juvenile survival of all three species in the population growth models, and used our observed reproduction values in the population growth models.

RESULTS

Distribution and Abundance

Ovenbird. Ovenbirds were more abundant in WI than MO (region effect, P = 0.0001, Table 2), but abundance did not differ between fragmented and contiguous forests (landscape effect, Table 2, P = 0.77). In MO, defections averaged 0.80 and 0.72 in fragmented and contiguous forests respectively, whereas in WI defections averaged 2.44 and 2.39 on fragmented and contiguous forests respectively (Table 3). Ovenbirds were more abundant in 1992 than 1991 (year effect, Table 2, P = 0.0001), but this increase was most apparent in WI (region x year interaction, Table 2, P = 0.0001), and particularly in the unfragmented WI forests where mean defections increased from 1.78 to 3.00 defections per 10 minute count (region x landscape x year interaction, Tables 2 and 3, P = 0.0002).

Red-eyed Vireo. Red-eyed Vireo abundance varied with the region and landscape (region x landscape interaction, Table 2, P = 0.0001). In WI, vireo abundance averaged 1.82 and 2.19 defections per count on fragmented and contiguous forests respectively (Table 3). In MO, however, vireo abundance dropped from an average of 2.52 defections per count on contiguous forest plots to 0.70 defections per count on fragments (Table 3).

Red-eyed vireos increased from 1991 to 1992 on all four study areas (year effect, Tables 2 and 3, P = 0.0001).

Wood Thrush. Wood Thrushes were more abundant in MO than WI (region effect, Table 2, P = 0.045), and on fragments than contiguous forests (landscape effect, Table 2, P = 0.0087). In MO, Wood Thrush abundance averaged 0.47 and 0.26 on fragmented and contiguous forests respectively (Table 3). Similarly, Wood Thrush abundance in WI averaged 0.34 and 0.09 on fragmented and contiguous forests respectively (Table 3). Wood Thrush abundance declined from 1991 to 1992 (year effect, Table 2, P = 0.0246), but this decline was most apparent in MO (region x year interaction, Table 2, P = 0.0183), where abundance decreased from 0.41 to 0.31 (Table 3).

Reproductive Success and Limiting Factors of Reproduction

The Chi-Square analyses used to determine if daily survival and cause-specific daily survival differed among the four populations, among fragmented and contiguous forests, and among regions was not a statistically powerful test. For example, when the Type I error rate was 0.1, the power of the Chi-Square test to detect a 0.02 difference in daily survival among populations was 0.12. Thus, if populations truly had different survival rates, we had a low probability of detecting these differences and a high probability (0.88) of concluding that true differences did not exist (Type B error). Interpretation of non significant differences in daily survival should be made in light of the high Type II error rate .

Ovenbird. Daily mortality of Ovenbird nests did not differ significantly among the four study areas (Omnibus Chi-Square = 3.73*,* Table 4, P = 0.29). In MO, nest failure (= the probability that a nest would not fledge any young) was 0.730 and 0.620 on fragments and contiguous sites respectively (Table 5). Similarly, in WI, nest failure was 0.803 and 0.579 on fragments and contiguous sites respectively (Table 5).

Daily mortality due to nest depredation accounted for the majority of nest failures (the failure of a nest to fledge at least one host offspring) in all four study areas, but did not differ between regions (Chi-Square = 0.06, P = 0.80) or with landscapes (Chi-Square = 2.28, P = 0.13, Table 4). Daily mortality due to nest abandonment was the second largest factor in nest failures and differed among the four study areas (Table 4, omnibus Chi Square =13.13, P = 0.0044). Abandonment was a cause of failure in all study areas except the MO fragments (Table 4). Abandonment did not differ between regions (Chi Square = 1.02, P = 0.31) or with landscapes (Chi-Square =1.58, P = 0.21, Table 4).

Daily mortality due to cowbird parasitism and stochastic causes did not differ among the four study areas (omnibus ChiSquare = 2.80, P = 0.42, omnibus Chi-Square = 067, P = 0.88, respectively, Table 4). Failure by parasitism was a factor only in fragments, where 16.7% and 5.27% of daily mortality was attributed to parasitism in MO and WI, respectively (Table 4). Failure due to stochastic events was recorded only in WI, accounting far 5.27% and 5.06% of daily mortality on fragments and contiguous forests there (Table 4). These estimates were not different from the MO populations (region ChiSquare = 1.81, P = 0.18).

Parasitism rates were low in contiguous forests; 1/40 (2.5%) and 2/50 (4%) nests were parasitized in MO and WI forests, respectively (Figure 1). On fragments, 8/12 (67%) and 6/31 (19%) nests were parasitized in MO and WI, respectively (Figure 4a). Across all study areas, sixty-seven nests successfully fledged at least one Ovenbird young. Of those nests, the mean number of Ovenbird fledglings in parasitized nests was lower (2.00) than the mean number of Ovenbird fledglings in non-parasitized nests (4.16, T = 5.41, P = .0001 Figure 2).

Red-eyed Vireo. Daily mortality of Red-eyed Vireo nests did not differ significantly among the four study regions (omnibus Chi-Square = 3.12, P = 0.37, Table 4). In MO, nest failure was 0.991 and 0.686 on fragments and contiguous sites respectively (Table 5). In WI, nest failure was 0.735 and 0.495 on fragments and contiguous sites respectively (Table 5).

Daily mortality due to nest depredation accounted for the majority (?50%) of nest failures in all four study areas, but did not differ between regions (Chi-Square =1.96, P = 0.16) or with landscapes (Chi-Square = 1.96, P = 0.16, Table 4). Nest predation accounted for 50% of daily mortality in WI contiguous forests, and > 80% of daily mortality in the other three study areas (Table 4).

Daily mortality due to nest abandonment did not differ among the four study areas (omnibus Chi-Square = 0.04, P = 0.99) or between regions (region Chi-Square = 0.98, P = 0.32). Nest abandonment was greater in unfragmented landscapes than fragmented F landscapes, (landscape Chi-Square = 2.83, P = 0.09, Table 4), where failures due to abandonment accounted for 7.66% and 50% of daily mortality in MO and WI contiguous habitats, respectively (Table 4).

We recorded nest failure due to cowbird parasitism only in WI fragments, where 19.96% of daily mortality was attributed to parasitism (Table 4). Daily mortality due to parasitism did not differ among the four study areas (omnibus Chi-Square = 1.06, P = 0.78), between regions (Chi-Square = 2.02, P = 0.155), or between landscapes (Chi Square = 2.02, P = 0.155, Table 4) Nest failure due to stochastic causes was not detected in any of the four study areas (Table 4).

Eleven percent (3/28) of Red-Eyed Vireo nests were parasitized in MO contiguous forests, and no nests (0/11) were parasitized in WI contiguous forests (Figure 1). On MO fragments, only two vireo nests were located, and one was parasitized. On WI fragments, 66.7% (8/12) nests were parasitized (Figure 1). Across all study areas, 24 nests successfully fledged at least one vireo young. Of those nests, the mean number of vireo fledglings in parasitized nests (2.4) did not differ from the mean number of vireo fledglings in non-parasitized nests (3.0; T = 1.12, P = 0.277, Figure 2).

Wood Thrush. Daily mortality of Wood Thrush nests did not differ significantly among the four study areas (omnibus Chi-Square = 3.86, P = 0.27) or between regions (Chi-Square = 0.80, P = 0.37). However, daily mortality differed between landscapes (Chi-Square = 2.98, P = 0.08, Table 4). In MO, nest failure was 0.732 and 0.568 on fragmented and contiguous plots respectively, and in WI nest failure was 0.681 and 0.399 on fragmented and contiguous plots, respectively (Table 5).

Failure due to nest predation accounted for $\geq$ 50% of daily mortality in all four study areas, but did not differ among populations (omnibus Chi-Square = 2.51, P = 0.47, Table 4). Failure due to abandonment accounted for 11 % to 33.5% of daily mortality in both WI study areas and MO contiguous forests, but was not detected in MO fragments (Table 4). Failures due to stochastic events were detected in MO contiguous and WI fragments, where 5.8% and 11.1% of daily mortality was caused by stochastic events (Table 4). Failures due to abandonment and stochastic causes did not differ among the four study areas, between regions, or between landscapes (P > 0.1 for all tests, Table 4).

Failure due to Cowbird parasitism differed among the four study areas (omnibus Chi-Square = 7.47, P = 0.0584). Fragments had higher daily mortality due to parasitism than contiguous forests (landscape Chi-Square = 7.42, P = 0.0065, Table 4). On fragments, parasitism accounted for 31.6% and 22.3% of daily mortality in MO and WI respectively (Table 4). Alternatively, failures due to cowbird parasitism were not detected on contiguous forests in WI or in MO (Table 4).

Parasitism of Wood Thrush nests was low to absent in contiguous forests; 1 of 55 (1.8%) nests in MO and 0 of 9 nests in WI contained cowbird eggs or young. Conversely, 81% (29/36) and 44% (8/18) of nests on fragments in MO and WI contained cowbird eggs or young (Figure 1). Across all study areas, sixty-one nests successfully fledged at least one Wood Thrush young. Of those, parasitized nests fledged significantly fewer (2.07) Wood Thrushes than non-parasitized nests (2.94, T = 2.9, P = 0.0049, Figure 2).

Generalized Patterns of Daily Survival and Nesting Success

Results of the Combined Probabilities Test indicated that daily mortality of nests was more closely associated with landscape than with region. Daily nest mortality was greater on fragments than contiguous forests (Chi-Square = 12.41, P = 0.053, Table 4), but did not differ among regions (Chi-Square = 5.41, P = 0.49, Table 4). Nest failures due to predation and parasitism were greater on fragments than contiguous forests (Chi Square =10.85, P = 0.093 and Chi-Square =17.08, P = 0.009, respectively; Table 4), whereas failures due to predation and parasitism did not differ between regions (Chi Square = 6.49, P = 0.37 and Chi-Square = 6.18, P = 0.40, respectively). Failures due to abandonment and stochastic events did not differ between landscapes (Chi-Square = 10.42, P = 0.11 and Chi-Square =1.86, P = 0.76, respectively) or with regions (Chi-Square = 5.29, P = 0.51 and Chi-Square = 4.51, P = 0.31, respectively).

Neotropical Migrant Viability

Ovenbird. Adult survival estimates for the Ovenbird were highly variable across studies (Table 6), ranging from 0.845 (Roberts 1971) to 0.540 (Savidge and Davis 1974). When the adult survival value of 0.845 was used (and juvenile survival is 0.31), all four study populations produced enough young to sustain the populations (Figure 5a).

Alternatively, when the adult survival value of 0.540 was used, none of the populations produced enough young to sustain the populations, and the populations were classified as sinks (Figure 3a).

When the mean adult survival was used (0.623) and juvenile survival was 0.31, recruitment of 1.2 female fledglings per year was required for population maintenance (Table 6). Mean female fledglings per year was 1.44 and 1.16 on MO and WI contiguous forests, respectively, and 0.79 and 0.74 on MO and WI fragments, respectively (Table 6). Because fledging success was lower for Ovenbirds in fragments, populations in fragments in both MO and WI/MN were more likely to be sinks than populations in contiguous forests.

When the mean demographic values were used in population growth models, Ovenbird populations on fragments in both regions declined to near extinction within 20 years in the absence of immigration (Figure 3b). Populations on contiguous forests slowly decreased over time in WI, but this decline reflected only a 0.04 deficit in female fledglings per female from the break-even point (Table 6). Ovenbird populations on contiguous forests in MO dramatically increased within 20 years (Figure 3b).

Red-eyed Vireo. Annual adult survival estimates for the Red-eyed Vireo ranged from 0.53 to 0.59 (mean survival estimate = 0.56, Table 6). When juvenile survival was 0.31, then the contiguous populations in both MO and WI were classified as potential sources for all estimates, whereas fragmented populations in MO and WI were classified as sinks (Figure 5c).

When the mean adult survival was used (0.56) and juvenile survival was 0.31, recruitment of 1.47 female fledglings per female per year was needed to balance adult mortality. Mean female fledglings per year was 1.57 and 1.82 on MO and WI contiguous forests respectively, and 0 and 0.38 on MO and WI fragments respectively (Table 6). Because fledging success was lower for Red-eyed Vireos in fragments, populations in fragments in both MO and WI/MN were more likely to be sinks than populations in contiguous forests (Figure 3a).

When the mean demographic values were used in population growth models, populations on fragments in both regions declined to near extinction within 20 years, whereas populations on contiguous forests in WI and MO increased over time and potentially served as sources (Figure 3d).

Wood Thrush. Annual adult survival rates for Wood Thrush varied from 0.58 i (Roth and Johnson 1993) to 0.80 (Robinson, unpubl.). When the adult survival rate of 0.80 was used, all four populations produced enough young to compensate for adult mortality (Figure Se). When the adult survival of 0.58 was used, fragments in both MO and WI were classified as sinks, whereas contiguous forests in MO and WI were classified as sources (Figure Se).

When the average adult survival value of 0.67 and fledgling survival value of 0.31 were used, a recruitment of 1.06 female offspring per adult female per year was needed to compensate for adult mortality (Table 6). Mean female fledglings per year was 2.04 and 2.71 on MO and WI contiguous forests respectively, and 0.94 and 1.13 on MO and WI fragments respectively (Table 6). Populations on contiguous forests in both MO and WI were classed as sources, while populations on WI fragments apparently broke even and populations on MO fragments were sinks. Because fledging success was lower for Wood Thrushes in fragments, populations in fragments in both MO and WI/MN were more likely to be sinks than populations in contiguous forests.

When we modeled population growth with those demographic values, and in the absence of immigration or emigration, populations on contiguous forests dramatically increased over time, whereas growth on WI fragments was low relative to population growth on contiguous habitat and growth on MO fragments was slightly negative (Figure

DISCUSSION

Distribution and Abundance

Because our primary goal was to document reproductive success on fragments and contiguous forests in two regions, we purposely studied fairly large fragments to avoid the greatly reduced densities (Wenny et al. 1993) and rates of pairing success (Gibbs and Faaborg 1990, Van Horn et al. 1994) found on smaller fragments in the Midwest. Thus, given large fragment size, we did not expect that distribution would be significantly affected by fragmentation. Yet, adult Ovenbird, Red-eyed Vireo, and Wood Thrush showed different distributional responses to fragmentation; Ovenbirds showed no response in either MO or WI, Red-eyed Vireos were less abundant on MO fragments but not on WI fragments, and Wood Thrushes were more abundant on both WI and MO fragments compared to contiguous habitats.

The distribution of these species on fragmented and contiguous forests in WI and MO may reflect either the distribution of required resources and how the resources vary geographically (Brown 1984) or historical differences in reproductive success across the regions studied. For example, the Wood Thrush population censused on fragments in MO may reflect birds that successfully raised offspring and returned in successive years, or it may comprise a population of immigrant Wood Thrushes that dispersed to apparently suitable habitat within the fragments we studied.

Because birds are highly vagile organisms, distributional differences may not reflect a population's ability to sustain itself (Pulliam 1988). If populations consist of a pool of immigrants that have "rescued" fragments from extinction (Brown and Kodric-Brown 1977), occurrence and density may be misleading indicators of habitat quality and productivity (Van Horn 1983, Pulliam 1988, and below). Thus, documentation of reproductive success can provide insights into why populations are distributed as they are on fragmented and contiguous forests.

Reproductive Success and Limiting Factors of Reproduction

Our results support the hypothesis that fragmentation of breeding habitat reduces the reproductive success of forest-nesting migratory birds. The combined probabilities from the independent tests for each species showed that the daily nest mortality was greater in fragmented habitats than contiguous habitats. These differences in daily nest mortality were greater between landscapes than between regions, suggesting that, within the Midwestern United States, habitat patterns affect migrant bird reproduction more than differences in geographic location. The increase in daily mortality on fragments was caused by increased nest predation and parasitism there. We suggest that landscape features in fragmented habitats may be more suitable for predator and parasite populations than unfragmented landscapes (Thompson et al. in press, Donovan et al. in press).

Independent analyses of all three species showed that daily nest mortality tended to be higher ($0.10 < P < 0.22$) on fragments compared to contiguous habitats in both WI and MO. There are two ways to interpret the non-significant landscape trends when analyzed on a per-species basis. First, Mayfield daily nest mortality and nest failure may truly differ between the populations, but our sample sizes and observation days may have been too small to detect these differences (i.e., the probability of detecting a difference of 0.02 in daily nest survival was 0.12; Power = 0.88). Alternatively, hayfield daily nest survival may not truly differ between these populations for the following reasons. We measured daily nest survival as the probability that a nest would fledge at least one host young. This (hayfield) method has been the traditional way of estimating nesting success because most nest failure is due to predation, and predation is often an all or nothing event. Eggs within a nest are not independent sampling units - if one egg is depredated it is likely other eggs within the same nest will also be depredated. For this reason, most investigators report nesting success on a per nest basis and ignore partial nest losses. The number of nests that failed to fledge at <u>least</u> one host young may, in fact, not differ between fragmented and contiguous forests. However, partial nest loss can influence the ability of a population to maintain itself over time by reducing the number of female fledglings per female. Cowbirds often remove a subset of host eggs and replace them with their own. Thus, removal of host eggs by cowbirds often only partially destroys a nest, but the effects of partial nest loss are not detected when nesting success is calculated on a per nest basis.

Partial nest failure due to cowbird parasitism reduced the number of offspring for Wood. Thrush and Ovenbird, but not for the Red-eyed Vireo. We suspect that, with larger samples, the vireo would show the same trend. All three species were parasitized by Brown-headed Cowbirds, and parasitism rates were higher on fragments than contiguous forests. Other studies on midwestern fragments also show that Ovenbird, Red-eyed Vireo, and Wood Thrush nests are heavily parasitized (Robinson 1992, Thompson et al., in press, Robinson ex al., manuscript). By examining only nests that successfully fledged host young (and assuming that daily mortality did not differ between fragmented and contiguous populations), we determined that partial nest loss due to cowbird parasitism reduces productivity on fragments.

Although fewer young were produced per adult on fragments compared to contiguous forests, the factors resulting in lower recruitment of Neotropical migrants on fragments appear to be species-specific. Predation reduced the nesting success of Ovenbirds and Red-eyed Vireos on fragments, and cowbird parasitism reduced the mean number of fledglings per nest. By contrast, Wood Thrush nesting success was significantly reduced by cowbird parasitism, decreasing the probability that a Wood Thrush nest would fledge at least one Wood Thrush and decreasing the mean number of offspring in nests that were successful. Thus, fragmentation negatively affected reproduction in all three species, but the mechanism of this reduction varied among species.

Conservation Implications: Population Viability in Fragmented and Contiguous Forests

Our results suggest that fragmentation reduces both the probability that a nest will successfully fledge at least one host offspring and the mean number of offspring produced per nest. We suggest that migratory bird populations nay be structured as a network of sources and sinks, where more productive source areas effectively subsidize or rescue unproductive sink areas (Pulliam 1988, Brown and Kodric-Brown 1977, Stacey and Taper 1991, Rolstad 1991). If so, the relevant demographic unit for long-term management of these species is the broader metapopulation, a system of subpopulations that are linked by dispersing individuals (Levins 1969, 1970, Hanski and Gilpin 1991).

Metapopulation theory considers a large number of patches, some which are occupied and some which are not (based on presence and absence data). Patches regularly go extinct and are recolonized, and although the pattern of occupancy is continually shifting, the proportion of sites that are occupied remains constant over time when the metapopulation is at equilibrium (Levins 1970). We are aware of only one study to date that explicitly examined the metapopulation dynamics of migratory passeriformes (Villard et al. 1992). In that study, birds were surveyed on 71 forest patches of varying size during two consecutive breeding seasons, and the investigators found that populations on small i fragments regularly go extinct and are recolonized according to metapopulation theory (Villard et al. 1992). They concluded that migratory birds exhibit the demographic features of a metapopulation, and that patch area is an important parameter in predicting whether populations undergo local extinction. Our results suggest that increased nest predation and brood parasitism are the mechanisms by which small patches go extinct and contribute to metapopulation dynamics.

If demography of some migrant bird populations is regulated in a source-sink fashion, then appropriate long-term conservation efforts must consider the consequences of metapopulation dynamics. Metapopulation dynamics have been modeled in an effort to determine the demographic and genetic significance of source-sink interactions. Numerically, a large proportion of a population may reside within sinks at any given time, and although sinks may not persist indefinitely, they can contribute significantly to metapopulation size and longevity (Pulliam 1988, Howe et al. 1991). Genetically, sinks may contribute to a more diverse gene pool (Lande and Barrowclough 1987), but this benefit is lost if immigrants and emigrants are not successfully exchanged among subpopulations (Howe et al. 1991). Management of sink populations, therefore, may be beneficial for some species.

Sinks may be a detriment, however, in that constant immigration from sources to sinks (fragments) may exert a negative influence on the larger population (Davis and Howe 1991, Donovan et al, manuscript). Demographically, sinks may be "draining" sources, resulting in widespread decline of some species across their geographic ranges. Thus, a clear understanding of Ovenbird, Red-eyed Vireo, and Wood Thrush population demography depends on examination of demographic dynamics within and among subpopulations that are linked by dispersal. Because habitat fragmentation has significant population ramifications for local Ovenbird, Red-eyed Vireo, and Wood Thrush populations, even on relatively large fragments, we suggest that the long-term viability of these species depends on maintaining large tracts of forest throughout the breeding range until the geographic scale at which source and sink populations interact can be determined.

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LITERATURE CITED

Askins, R. A., J. F. Lynch, and R. Greenberg. 1990. Population declines in migratory birds in eastern North America. Curr. Ornith. 7:1-57.

Bollinger, E. K., and E. T. Linder. 1994. Reproductive success of Neotropical migrants in a fragmented Illinois forest. Wilson Bull. 106:46-54.

Brown, J. H. 1984. On the relationship between abundance and distribution of species. Am. Nat. 124:255-279.

Brown, J. H., and A. Kodric-Brown. 1977. Turnover rates in insular biogeography: effect of immigration and extinction. Ecology 58:445-449.

Davis, G. J., and R. W. Howe. 1992. Juvenile dispersal, limited breeding sites, and the dynamics of metapopulations. Theor. Pop. Biol. 41:184-207.

Donovan, T. M., F. R. Thompson III, and J. Faaborg. In press. Ecological trade-offs and the influence of scale on Brown-headed Cowbird distribution. In The ecology and management of Cowbirds (T. L. Cook, ed.). University of Texas Press, Austin, Texas.

Ehrlich, P. R,, D. S. Dobkin, and D. Wheye. 1988. The birder's handbook. Simon and Schuster Inc., New York.

Faaborg, J., M. Brittingham, T. Donovan, and J. Blake. In review. Neotropical migrant responses to habitat fragmentation in the temperate zone. In Ecology and management of Neotropical migratory birds: A synthesis and review of the critical issues (D. Finch and T. Martin, eds.). Oxford University Press.

Finch, D. 1991. Population ecology, habitat requirements, and conservation of Neotropical migratory birds. USDA Forest Service, Rocky Mountain Forest and Range Experiment Station Gen. Tech. Rep. RM-205.

Gibbs, J. P., and J. Faaborg. 1990. Estimating the viability of Ovenbird and Kentucky warbler populations in forest fragments. Conserv. Biol. 4:193-196.

Greenberg, R. 1980. Demographic aspects of long-distance migration. Pages 493-504 in Migrant birds in the Neotropics: Ecology, behavior, distribution, and conservation (A. Keast and E. S. Morton, eds.). Smithsonian Institution Press, Washington, D.C.

Greenwood, P. J., and P. H. Harvey. 1982. The natal and breeding dispersal of birds. Ann. Rev. Ecol. Syst. 13:1-21.

Hann, H. W. 1937. Life history of the Ovenbird in southern Michigan. Wilson Bull. 181:145-236.

Hanski, L, aid M. Gilpin. 1991. Metapopulation dynamics: Brief history and conceptual domain. Biol. J. Linnean Soc. 42:316.

Harris, L.D. 1984. The fragmented forest: Island biogeographic theory and preservation of biotic diversity. Univ. Chicago Press, Chicago, Illinois.

Holmes, R. T., and T. W. Sherry. 1992. Site fidelity of migratory warblers in temperate breeding and Neotropical wintering areas: Implications for population dynamics, habitat selection, and conservation. Pages 563-575 in_ Ecology and conservation of Neotropical migrant landbirds (J. M. Hagan and D. W. Johnson, eds.). Smithsonian Institute Press, Washington, D. C.

Hoover, J. P., M. C. Brittingham, and L. J. Goodrich. In press. Nesting success of Wood Thrushes in a fragmented forest landscape in Pennsylvania. Auk.

Howe, R. W., G. J. Davis, and V. Mosca. 1991. The demographic significance of 'sink' populations. Biol. Conserv. 57:239-255.

Lande, R. L., and G. G. Barrowclough. 1987. Effective population size, genetic variation, and their use in management. Pages 87-123 in_ Viable populations for conservation (M. E. Soule, ed.). Cambridge University Press, New York.

Levins, R. 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. Bull. Entomol. Soc. Amer. 15:237-240.

Levins, R. 1970. Extinction. Pages 77-107 'fir Some mathematical problems in biology. (M. Gerstenhaber, ed.). American Mathematical Society, Providence, Rhode Island.

Lowther, P. 1993. Brown-headed Cowbird (Molothrus ater). In The Birds of North America (A. Poole and F. Gill, eds.). Philadelphia: The Academy of Natural I

Sciences: American Ornithologists Union.

Mayfield, H.F. 1975. Suggestions for calculating nest success. Wilson Bull. 87:456466.

Martin, T. E. 1992. Breeding productivity considerations: what are the appropriate habitat features for management? Pages 455-473 in Ecology and conservation of Neotropical migrant landbirds (J. M. Hagan III and D. W. Johnson, eds.). Smithsonian Institute Press, Washington D.C.

Martin, T. E. In press. Variation and covariation of life history traits m birds in relation to nest sites, nest predation, and food. Ecological Monographs.

Nichols, J. D., B. R. Noon, S. L. Stokes, and J. E. Hines. 1981. Remarks on the use of mark-recapture methodology in estimating avian population size. Studies in Avian Biology 6:121-136.

Paton, P. W. 1994. The effect of edge on avian nest success: How strong is the evidence? Conserv. Biol. 8:17-26.

Peterjohn, B. G., and J. R. Sauer. 1994. Population trends of woodland birds from the North American Breeding Bird Survey. Wildl. Soc. Bull. 22:155-164.

Porneluzi, P., J. C. Bednarz, L. Goodrich, N. Zawada, and J. Hoover. 1993. Reproductive performance of territorial Ovenbirds occupying forest fragments and a contiguous forest in Pennsylvania. Conserv. Biol. 7:618-622.

Pulliam, H. R. 1988. Sources, sinks, and population regulation. Am. Nat. 132:652-661.

Rickleffs, R. L. 1973. Fecundity, mortality, and avian demography. Pages 366-435 'fin Breeding biology of birds (D.S. Farner, ed.). National Academy of Science.

Robbins, C. S. 1979. Effect of forest fragmentation on bird populations. US Dept. of Agriculture, Forest Service General Technical Report NC-51.

Robbins, C. S., J. R. Sauer, R Greenberg, and S. Droege. 1989. Population declines in North American birds that migrate to the Neotropics. Proc. Natl. Acad. Sci. 86.

Roberts, J. O. L. 1971. Survival among some North American wood warblers. Bird Banding 42:165-183.

Robinson, S. K. 1992. Population dynamics of breeding Neotropical migrants in a fragmented Illinois landscape. Pages 408-418 in n Ecology and conservation of Neotropical migrant landbirds (J. M. Hagan and D. W. Johnston, eds.). Smithsonian Institution Press, Washington and London.

Robinson, S. K., J. A. Grzybowski, S. I. Rothstein, M. C. Brittingham, L. J. Petit, and F. R. Thompson. 1993. Management implications of Cowbird parasitism for neotropical migrant songbirds. In Status and management of Neotropical migratory birds (D. Finch and P. Stengel, eds.). USDA Forest Service Rocky Mountain Forest and Ranga Experiment Station. Fort Collins, Colorado.

Rolstad, J. 1991. Consequences of forest fragmentation for the dynamics of bird populations: Conceptual issues and the evidence. Biol. J. Linnean Soc. 42:149-163.

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.

Sauer, J. R., and B. K. Williams. 1989. Generalized procedures for testing hypotheses about survival or recovery rates. J. Wildl. Manage. 53:137142.

Savidge, I. R., and D. E. Davis. 1974. Survival of some common passerines in a Pennsylvania woodlot. Bird-Banding 45:152-155.

Sherry, T. W., and R. T. Holmes. 1992. Population fluctuations in a long-distance Neotropical migrant: Demographic evidence for the importance of breeding season events in the American Redstart. Pages 431-44.2 irk Ecology and conservation of

Neotropical migrant landbirds (J. M. Hagan III and D. W. Johnston, eds.). Smithsonian Institution Press, Washington, D. C.

Sherry, T. W., and R. T. Holmes. 1993. Are populations of Neotropical migrant birds limited in summer or winter? Implications for management. In Status and management of Neotropical migratory buds (D. Finch and P. Stengel, eds.). USDA Forest Service Rocky Mountain Forest and Range Experiment Station. Fort Collins, Colorado.

Sokal, R. R., and F. J. Rohlf 1981. Biometry, 2nd ed. W. H. Freeman and Company, New York.

Stacey, P. B., and M. Taper. 1992. Environmental variation and the persistence of small populations. Ecol. Applic. 2:18-29.

Temple, S. A., and J. R. Cary. 1988. Modeling dynamics of habitat-interior bird populations in fragmented landscapes. Conserv. Biol. 2:340347.

Thompson, F. R., S. J. Lewis, J. Green, and D. Ewert. 1993. Status of Neotropical migrant landbirds in the Midwest: identifying species of management concern. In Status and management of Neotropical migratory birds (D. Finch and P. Stengal, eds.). USDA Rocky Mountain Forest and Range Research Station. Fort Collins, Colorado.

Thompson, F. R. III. 1993. Simulated responses of a forest-interior bird population to forest management options in central hardwood forests of the United States. Conserv. Biol. 7:325-333.

Thompson, F. R. III, S. K. Robinson, T. M. Donovan, J. Faaborg, and D. R. Whitehead. In press. Biogeographic, landscape, and local factors affecting Cowbird abundance and host parasitism levels. In The ecology and management of Cowbirds (T. L. Cook, ed.). University of Texas Press, Austin, Texas.

Van Horn, B. 1983. Density as a misleading indicator of habitat quality. J. Wildl. Manage. 47:893-901.

Verner, J. 1988. Optimizing the duration of point counts for monitoring trends in bird populations. USDA Forest Service. NTIS, PSW - 395.

Verner, J. , and K. A. Mime. 1989. Coping with sources of variability when monitoring population trends. Ann. Zool. Fennici 26:191-199. .

Villard, M. A., K. Freemark, and G. Merriam. 1992. Metapopulation theory and Neotropical migrant birds in temperate forests: an emperical investigation. In Ecology and conservation of Neotropical migrant landbirds (J. M. Hagan and D.

L. W. Johnston, eds.). Smithsonian Institution Press, Washington D.C. Villard, M. A., P. R. Martin, and C. G. Dr Drummond. 1993. Habitat fragmentation and pairing success in the Ovenbird (Seiurus aurocapillus). Auk 110:759-768.

Wenny, D. G., R. L. Clawson, J. Faaborg, and S. L. Sheriff. 1993. Population density, habitat selection and minimum area requirements of three forest-interior warblers in central Missouri. Condor 95:968-979.

Wilcove, D. S., and S. K. Robinson. 1990. The impact of forest fragmentation on bird communities in eastern North America. Pages 319-331 in Biogeography and ecology of forest bird communities (A. Keast, ed.). SPB Academic Publishing, The Hague, The Netherlands.

Figure 1. Bars indicate parasitism rate, or the proportion of nests containing cowbird eggs or young in each study area. Line indicates the mean number of cowbirds detected per 10 minute census in each study area. Note the concordance between parasitism rate and cowbird detections per ten-minute count.

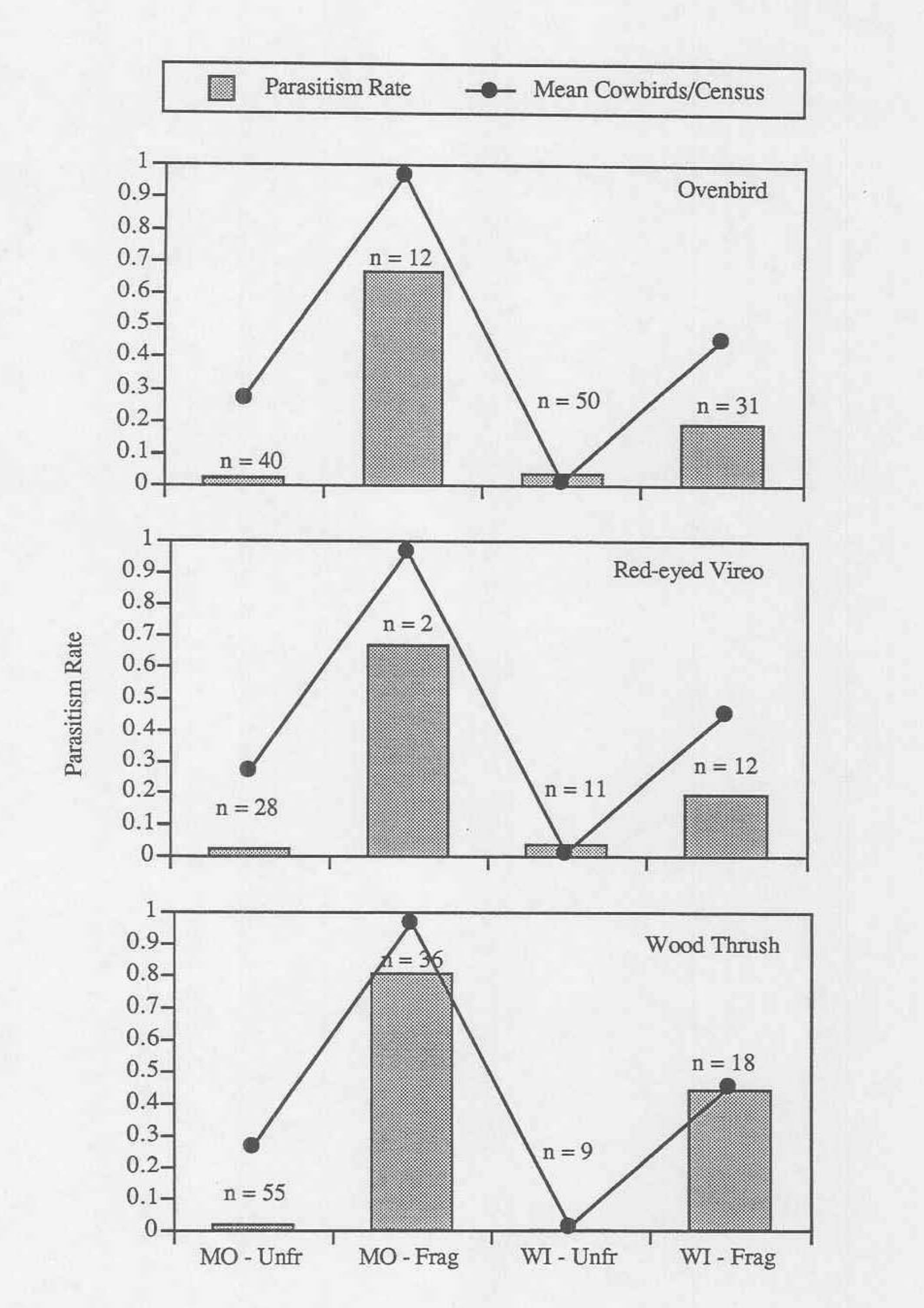
Parasitism Rate
Mean Cowbirds/Census
Ovenbird
Red-eyed Vireo
Wood Thrush
Parasitism Rate
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
n = 40
n = 12
n = 50
n = 31
n = 28
n = 2
n = 11
n = 12
n = 55
n = 36
n = 9
n = 18
MO - Unfr
MO - Frag
WI - Unfr
WI - Frag

Figure 2. The mean number and standard deviation of Ovenbird (OVEN), Red eyed Vireo (REVD, and Wood Thrush (WOTH) fledglings in non parasitized (solid) and parasitized (open) nests that successfully fledged at least one host young. Nest samples are combined across all study areas.

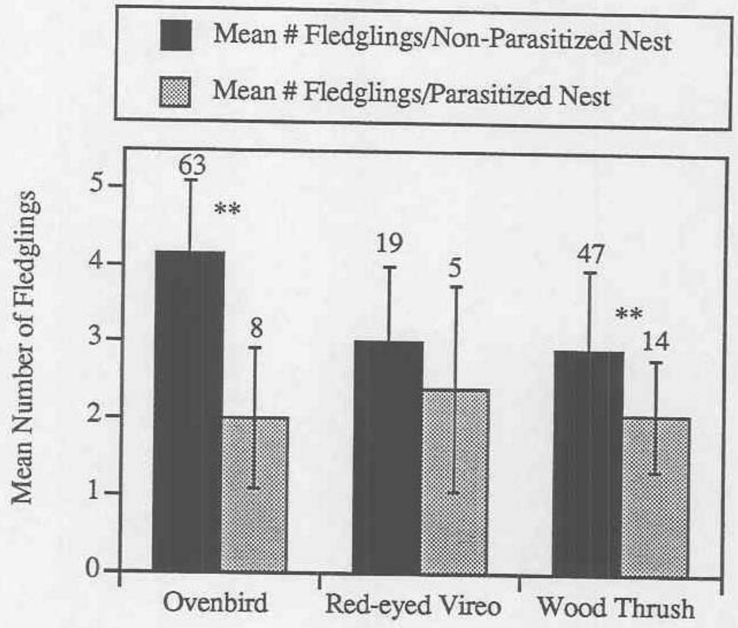■ Mean # Fledglings/Non-Parasitized Nest
▨ Mean # Fledglings/Parasitized Nest
Mean Number of Fledglings
0
1
2
3
4
5
63
**
8
19
5
47
**
14
Ovenbird
Red-eyed Vireo
Wood Thrush

Figure 3. a, c, e) The source sink status of Ovenbirds, Red eyed Vireos, and Wood Thrushes based on juvenile survivorship rate = 0.31; different published estimates of adult mortality are shown by different symbols. For example, the solid circle in panel 'a' represents population status of Ovenbirds in all four study areas based on Roberts (1971) estimate of adult survivorship = 0.845. Using Robert's estimate, all four study populations are classified as potential sources. The square figure in panel 'a' represents the population status of Ovenbirds in all four study areas based on Faaborg et al.'s (in press) estimate of adult survivorship = 0.57. Using Faaborg's estimate, the MO contiguous population is classified as a source, while the other three populations are classified as sinks.

3 b, d, f. Results of population simulations for the Ovenbird (panel b), Red eyed Vireo (panel d), and Wood Thrush (panel fj in the four study areas. Initial population size (year 1) was derived from area specific point count data * 1000.

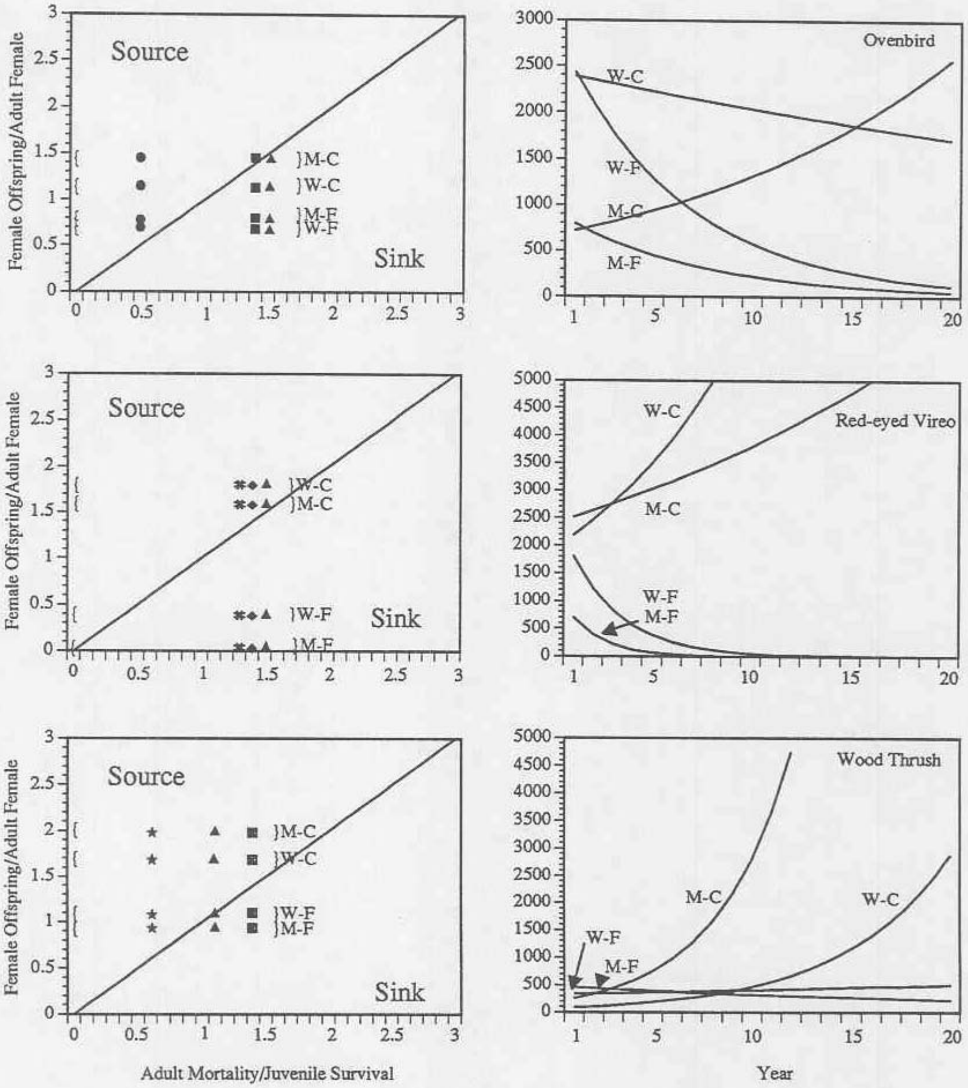
Source
Sink
Female Offspring/Adult Female
Adult Mortality/Juvenile Survival
}M-C
}W-C
}M-F
}W-F
Ovenbird
Red-eyed Vireo
Wood Thrush
W-C
W-F
M-C
M-F
Year
0
0.5
1
1.5
2
2.5
3
500
1000
1500
2000
2500
3000
3500
4000
4500
5000
5
10
15
20

Table 1. Location, habitat description, and landscape statistics of the 28 sites studied in Wisconsin/Minnesota (WI/MN) and Missouri (MO) in fragmented and contiguous landscapes. All statistics with a superscript 1 are based on habitat characteristics within a 10km radius surrounding each site. Sites in which nests were monitored have superscript of 2.

Site	Region	Landscape	UTM Coordinates Easting, Northing	% Forest Cover (ha)^1	Mean Patch Size (ha)^1	# of Patches (ha)^1	Edge Density (m/ha)^1	Mean Core Area Index (%)^1
Drummond-N	WI/MN	contiguous	5131750,628750	94.83	29800.0	1	2.94	74.46
Drummond-S^2	WI/MN	contiguous	5130600,628780	94.67	29750.0	1	3.02	73.99
Hardwoods-E^2	WI/MN	contiguous	5130900,652880	93.00	29225.0	1	3.56	70.72
Hardwoods-W^2	WI/MN	contiguous	5131050,652220	92.84	29175.0	1	3.69	70.09
Town Hall-N^2	WI/MN	contiguous	5116110,648010	91.01	28600.0	1	4.15	67.46
Town Hall-S	WI/MN	contiguous	5115350,647900	90.69	28500.0	1	4.23	66.98
			Mean	92.84	29175	1	3.60	70.62
			(SD)	(1.75)	(549.5)	(0)	(0.54)	(3.15)

Table 1. Continued.

County O	WI/MN	fragmented	5058105,509805	56.63	1782.5	10	3.99	40.98
Greenburg	WI/MN	fragmented	5007170,520110	23.83	202.70	37	8.94	2.54
Interstate[2]	WI/MN	fragmented	5026320,529435	25.02	281.25	28	7.99	3.81
O'Brien[2]	WI/MN	fragmented	5008325,516495	23.75	182.32	41	8.69	2.54
Wild Mtn[2]	WI/MN	fragmented	5036810,522150	25.34	398.75	20	7.32	3.73
Wild River[2]	WI/MN	fragmented	5040990,520700	33.28	455.43	23	6.94	11.52
			Mean	31.31	550.49	26.50	7.31	10.85
			(SD)	(12.91)	(613.01)	(11.40)	(1.80)	(15.14)
Card-E	MO	contiguous	671454,4111952	95.31	29950.0	1	2.64	76.21
Card-W	MO	contiguous	670131,4112363	95.15	29900.0	1	2.66	76.37
Deer Run	MO	contiguous	673907,4116420	90.21	28350.0	1	4.61	66.03
Peck-NE	MO	contiguous	667337,4104973	95.86	28925.0	1	2.20	79.20
Peck-NW	MO	contiguous	666766,4104622	96.52	29150.0	1	2.09	79.55

Table 1. Continued.

Peck-SE	MO	contiguous	659745,4097685	95.62	18000.0	1	2.60	73.57
Peck-SW	MO	contiguous	659368,4098509	95.91	19950.0	1	2.38	75.12
Carr Creek	MO	contiguous	665388,4115224	95.86	30125.0	1	2.08	78.92
			Mean	95.06	26793.75	1	2.66	75.62
			(SD)	(2.00)	(4890.09)	(0)	(0.82)	(4.41)
Ashland Lake[2]	MO	fragmented	568726,4289831	43.52	1519.44	9	9.07	12.41
Ashland[2]	MO	fragmented	569488,4289198	43.20	1508.33	9	9.18	12.09
Bennitt[2]	MO	fragmented	547134,4344976	38.19	631.58	19	10.71	8.27
County-J	MO	fragmented	578138,4301920	20.22	225.89	28	7.39	2.96
Fulton	MO	fragmented	590714,4305856	21.42	231.03	29	6.97	3.36
Hung. Mother[2]	MO	fragmented	538506,4343204	35.56	620.83	18	10.10	7.00
Millersburg	MO	fragmented	580595,4304509	16.23	169.17	30	6.20	1.92
Whetstone-E	MO	fragmented	613270,4311946	37.87	661.11	18	8.97	11.06
Whetstone-W	MO	fragmented	610686,4313712	32.06	503.75	20	7.80	9.23
		Mean		32.03	674.57	20	8.49	7.59
		(SD)		(10.27)	(511.92)	(7.88)	(1.49)	(4.04)

Table 2. Repeated measure analysis of variance results, based on mean detections of Ovenbirds, Red-eyed Vireos, and Wood Thrushes in fragmented and contiguous forests (landscape effect) in Wisconsin and Missouri (region effect) in 1991 and 1992 (year effect).

SPECIES	FACTOR	DF	F	P
Ovenbird	Region	1	85.62	0.0001
	Landscape	1	0.08	0.7736
	Year	1	71.16	0.0001
	Region x Landscape	1	0.00	0.9769
	Region x Year	1	50.94	0.0001
	Landscape x Year	1	1.70	0.2052
	R x L x Y	1	20.16	0.0002
Red-eyed Vireo	Region	1	9.96	0.0041
	Landscape	1	70.80	0.0001
	Year	1	55.73	0.0001
	Region x Landscape	1	29.68	0.0001
	Region x Year	1	0.40	0.5328
	Landscape x Year	1	3.26	0.0847
	R x L x Y	1	3.57	0.0723
Wood Thrush	Region	1	4.44	0.0452
	Landscape	1	8.11	0.0087
	Year	1	5.91	0.0246
	Region x Landscape	1	0.20	0.6585
	Region x Year	1	6.60	0.0183
	Landscape x Year	1	0.34	0.5671
	R x L x Y	1	0.07	0.7954

Table 3. Mean detections and standard deviation (SD) per 10 minute census of selected species within 50m, 70m, and unlimited distance on fragmented (FRAG) and contiguous (UNFR) forests in Wisconsin/Minnesota (WI/MN) and Missouri (MO) in 1991 and 1992.

SPECIES	REGION	LAND-SCAPE	YEAR	N	MEAN (<50M)	SD (<50M)	MEAN (<70M)	SD (<70M)	MEAN (ALL)	SD (ALL)
Ovenbird	MO	FRAG	1991	9	0.21	0.10	0.45	0.20	0.69	0.32
			1992	8	0.35	0.16	0.60	0.24	0.91	0.35
		UNFR	1991	6	0.30	0.22	0.56	0.33	0.69	0.38
			1992	8	0.19	0.13	0.36	0.22	0.74	0.42
	WI/MN	FRAG	1991	6	0.75	0.11	1.43	0.22	2.16	0.58
			1992	6	1.08	0.33	1.68	0.45	2.71	0.72
		UNFR	1991	6	0.64	0.19	1.21	0.41	1.78	0.45
			1992	6	1.28	0.37	2.11	0.51	3.00	0.68

Table 3. Continued.

Red-eyed Vireo	MO	FRAG	1991	9	0.25	0.10	0.37	0.13	0.46	0.18
			1992	8	0.51	0.20	0.73	0.29	0.94	0.34
		UNFR	1991	6	1.38	0.35	2.22	0.28	2.32	0.29
			1992	8	0.99	0.21	1.69	0.24	2.71	0.42
	WI/MN	FRAG	1991	6	0.69	0.34	1.32	0.42	1.66	0.61
			1992	6	0.73	0.21	1.18	0.23	1.97	0.40
		UNFR	1991	6	0.94	0.07	1.51	0.12	1.78	0.24
			1992	6	1.34	0.36	2.05	0.48	2.60	0.50
Wood Thrush	MO	FRAG	1991	9	0.29	0.12	0.39	0.18	0.52	0.26
			1992	8	0.13	0.11	0.23	0.16	0.41	0.28
		UNFR	1991	6	0.10	0.05	0.21	0.11	0.30	0.12
			1992	8	0.06	0.05	0.09	0.07	0.21	0.17
	WI/MN	FRAG	1991	6	0.08	0.05	0.17	0.12	0.33	0.15
			1992	6	0.07	0.03	0.13	0.08	0.34	0.28
		UNFR	1991	6	0.04	0.04	0.11	0.05	0.09	0.06
			1992	6	0.15	.	0.06	0.10	0.08	0.12

Table 4. Daily mortality of Ovenbird, Red-eyed Vireo, and Wood Thrush nests on fragmented and contiguous forests in Missouri and Wisconsin. Daily mortality is partitioned by cause of failure, shown in brackets. The omnibus tests for differences in daily mortality among the four study areas; region tests for differences between Missouri and Wisconsin; landscape tests for differences between populations on fragmented and contiguous forests.

			Daily Mortality				
Species	**Region**	**Land-scape**	**Failed by any cause**	**[Failed by Predation]**	**[Failed by Parasitism]**	**[Failed by Abandonment]**	**[Failed by Stochastic Causes]**
Ovenbird	MO	Frag	0.0508	[0.0424]	[0.0085]	[0]	[0]
	MO	Unfr	0.0384	[0.0274]	[0]	[0.0110]	[0]
	WI/MN	Frag	0.0626	[0.0461]	[0.0033]	[0.0099]	[0.0033]
	WI/MN	Unfr	0.0336	[0.0218]	[0]	[0.0101]	[0.0017]
		Omnibus	3.73, 3 (0.2918)	3.94, 3 (0.2681)	2.80, 3 (0.4236)	13.13, 3 (0.0044)	0.67, 3 (0.8804)
	X^2, df (P)	Region	0.06, 1 (0.8028)	0.006, 1 (0.9387)	0.32, 1, (0.5674)	1.02, 1 (0.3120)	1.81, 1 (0.1782)
		Landscape	2.28, 1 (0.1314)	2.58, 1 (0.1082)	1.69, 1 (0.1941)	1.58, 1 (0.2088)	0.19, 1 (0.6627)
Red-eyed Vireo	MO	Frag	0.1600	[0.1600]	[0]	[0]	[0]
	MO	Unfr	0.0418	[0.0386]	[0]	[0.0032]	[0]
	WI/MN	Frag	0.0481	[0.0385]	[0.0096]	[0]	[0]
	WI/MN	Unfr	0.0248	[0.0124]	[0]	[0.0124]	[0]
		Omnibus	3.12, 3 (0.3728)	6.31, 3 (0.0974)	1.06, 3 (0.7845)	0.04, 3 (0.9976)	-
	X^2, df (P)	Region	1.48,1 (0.2241)	1.96, 1 (0.1613)	2.02, 1 (0.1551)	0.98, 1 (0.3234)	-
		Landscape	1.78, 1 (0.1822)	1.96, 1 (0.1620)	2.02, 1 (0.1551)	2.83, 1 (0.0926)	-

Table 4. Continued.

Wood	MO	Frag	0.0456	[0.0312]	[0.0144]	[0]	[0]
Thrush	MO	Unfr	0.0312	[0.0220]	[0]	[0.0073]	[0.0018]
	WI/MN	Frag	0.0398	[0.0221]	[0.0089]	[0.0044]	[0.0044]
	WI/MN	Unfr	0.0182	[0.0121]	[0]	[0.0061]	[0]
		Omnibus	3.86, 3 (0.2741)	2.51, 3 (0.4740)	7.47, 3 (0.0584)	6.03, 3 (0.1099)	1.3, 3 (0.7187)
	X^2, df (P)	Region	0.80, 1 (0.3700)	1.28, 1 (0.2577)	0.42, 1 (0.5162)	0.14, 1 (0.7052)	0.29, 1 (0.5879)
		Landscape	2.98, 1 (0.0843)	1.31, 1 (0.2517)	7.42, 1 (0.0065)	1.16, 1 (0.2814)	0.29, 1 (0.5879)
Combined	$-2\sum \ln P$,df,	Region	5.42, 6 (0.491)	6.49, 6 (0.371)	6.18, 6 (0.403)	5.29, 6 (0.508)	4.51, 4 (0.314)
Probability	(P)	Landscape	12.41, 6 (0.053)	10.85, 6 (0.093)	17.08, 6 (0.009)	10.43, 6 (0.108)	1.19, 4 (0.757)

Table 5. Daily nest survival, variance of daily nest survival, and the probability that a nest will successfully fledge (=nesting success) or fail (= nest failure) of Ovenbirds, Red-eyed Vireos, and Wood Thrushes. Regions are Missouri (MO) and Wisconsin/Minnesota (WI/MN); Landscapes are fragmented (FRAG) or unfragmented (UNFR). N = total nest sample size, Obs. Days = the total number of observation days pooled across all nests within the study area.

Species	Region	Land-scape	N	Obs. Days	Daily Survival	Daily Survival Variance	Daily Mortality	Nest Failure
Ovenbird	MO	FRAG	15	118.0	0.949	0.0004	0.051	0.730
		UNFR	40	364.5	0.962	0.0001	0.038	0.620
	WI/MN	FRAG	36	303.5	0.937	0.0002	0.063	0.803
		UNFR	51	596.5	0.966	0.00005	0.034	0.579
Red-eyed Vireo	MO	FRAG	2	12.5	0.940	0.011	0.160	0.991
		UNFR	34	311.0	0.958	0.0001	0.042	0.686
	WI/MN	FRAG	13	208.0	0.952	0.0002	0.048	0.735
		UNFR	13	161.5	0.975	0.0002	0.025	0.495
Wood Thrush	MO	FRAG	36	417.0	0.954	0.0001	0.046	0.732
		UNFR	56	545.5	0.969	0.0001	0.031	0.586
	WI/MN	FRAG	22	226.0	0.960	0.0002	0.040	0.681
		UNFR	9	165.0	0.982	0.0001	0.018	0.399

Table 6. Demographic parameters used in assessing source-sink status for the Ovenbird (OVEN), Red-eyed Vireo (REVI), and Wood Thrush (WOTH) in fragmented (Frag) and unfragmented (Unfr) habitats in Missouri (MO) and Wisconsin/Minnesota (WI/MN). The symbols associated with each reference are used in Figure 3.

OVEN	Adult Survival	Reference and Study Location	Juvenile Survival	Female F1 per Adult	Status
MO Frag	0.540	▲ Savidge and Davis 1974 (PA)	0.31	0.79	sink
	0.537	▲ Hann 1948 (MI)	0.31	0.79	sink
	0.57	■ Faaborg and Arendt, in press (PR)	0.31	0.79	sink
	0.845	● Roberts 1971 (MA)	0.31	0.79	source
Mean	0.623		0.31	0.79	sink
MO Unfr	0.540	Savidge and Davis 1974 (PA)	0.31	1.44	sink
	0.537	Hann 1948 (MI)	0.31	1.44	sink
	0.57	Faaborg and Arendt, in press (PR)	0.31	1.44	source
	0.845	Roberts 1971 (MA)	0.31	1.44	source
Mean	0.623		0.31	1.44	source
WI Frag	0.540	Savidge and Davis 1974 (PA)	0.31	0.74	sink
	0.537	Hann 1948 (MI)	0.31	0.74	sink
	0.57	Faaborg and Arendt, in press (PR)	0.31	0.74	sink
	0.845	Roberts 1971 (MA)	0.31	0.74	source
Mean	0.623		0.31	0.74	sink
WI - Unfr	0.540	Savidge and Davis 1974 (PA)	0.31	1.16	sink
	0.537	Hann 1948 (MI)	0.31	1.16	sink
	0.57	Faaborg and Arendt, in press (PR)	0.31	1.16	sink
	0.845	Roberts 1971 (MA)	0.31	1.16	source
Mean	.623		0.31	1.16	sink

Table 6. Continued

REVI					
MO Frag	0.53	▲ Savidge and Davis 1974 (PA)	0.31	0	sink
	0.57	◆ Nichols et al. 1981 (NH)	0.31	0	sink
	0.59	✱ Nichols et al. 1981 (MD)	0.31	0	sink
Mean	0.56		0.31	0	sink
MO Unfr	0.53	Savidge and Davis 1974 (PA)	0.31	1.57	source
	0.57	Nichols et al. 1981 (NH)	0.31	1.57	source
	0.59	Nichols et al. 1981 (MD)	0.31	1.57	source
Mean	0.56		0.31	1.57	source
WI Frag	0.53	Savidge and Davis 1974 (PA)	0.31	.384	sink
	0.57	Nichols et al. 1981 (NH)	0.31	.384	sink
	0.59	Nichols et al. 1981 (MD)	0.31	.384	sink
Mean	0.56		0.31	.384	sink
WI - Unfr	0.53	Savidge and Davis 1974 (PA)	0.31	1.82	source
	0.57	Nichols et al. 1981 (NH)	0.31	1.82	source
	0.59	Nichols et al. 1981 (MD)	0.31	1.82	source
Mean	0.56		0.31	1.82	source

Table 6. Continued.

WOTH					
MO Frag	0.58	☒ Roth and Johnson 1993 (DE)	0.31	0.94	sink
	0.64	▲ Savidge and Davis 1974 (PA)	0.31	0.94	sink
	0.80	★ Robinson unpubl. (IL)	0.31	0.94	source
Mean	.67		0.31	0.94	sink
MO Unfr	0.58	Roth and Johnson 1993 (DE)	0.31	2.04	source
	0.64	Savidge and Davis 1974 (PA)	0.31	2.04	source
	0.80	Robinson unpubl. (IL)	0.31	2.04	source
Mean	0.67		0.31	2.04	source
WI Frag	0.58	Roth and Johnson 1993 (DE)	0.31	1.134	source
	0.64	Savidge and Davis 1974 (PA)	0.31	1.134	sink
	0.80	Robinson unpubl. (IL)	0.31	1.134	source
Mean	0.67		0.31	1.134	source
WI - Unfr	0.58	Roth and Johnson 1993 (DE)	0.31	1.714	source
	0.64	Savidge and Davis 1974 (PA)	0.31	1.714	source
	0.80	Robinson unpubl. (IL)	0.31	1.714	source
Mean	0.67		0.31	1.714	source

CHAPTER VI

MODELING THE EFFECTS OF HABITAT FRAGMENTATION ON SOURCE AND SINK DEMOGRAPHY OF NEOTROPICAL MIGRANT BIRDS

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ABSTRACT

Many metapopulations are structured as a network of sources and sinks that are linked by dispersal. We used a modeling approach to examine explicitly how metapopulations respond to incremental fragmentation of source habitat and how this response may vary depending upon the life history attributes of a species. Fragmentation of source habitats led to a predictable decline in metapopulation size for all hypothetical species examined, but the manner in which populations declined varied from species to

species. When the source was "weak", producing few excess individuals, fragmentation of source habitats resulted in a predictable and parallel population decline of adults in both the source and the sink. In populations where sources produced many excess individuals, fragmentation of the source led to population declines in both the source and the sink, but this decline was more abrupt in sink habitats.

Fragmentation of source habitats differentially affected species with varying intrinsic rates of dispersal from one habitat type to another. When the sources are unfragmented and produce a large excess of individuals, intrinsic dispersal had little effect on metapopulation size and structure. However, as sources were fragmented and the reproductive excess of the source was diminished, metapopulation size dramatically declined in species with high intrinsic rates of dispersal. Species with high rates of dispersal experience a demographic cost by dispersing from high quality source habitat 'to low quality sink habitat.

INTRODUCTION

Many populations exist as metapopulations, or subpopulations that are linked by dispersal (Levins 1969, 1970, Hanski and Gilpin 1991). Metapopulation theory centers around the extinction and recolonization of subpopulations, and the study of metapopulation dynamics focuses on factors that influence these processes and the conditions in which these processes are balanced (Hanski and Gilpin 1991). Sources and sinks are one example of metapopulation dynamics, where the intrinsic growth rate of subpopulations varies among habitat types (Pulliam 1988). Sources are subpopulations that are demographically viable (juvenile production exceeds adult mortality), while sinks are subpopulations that are demographically inviable (juvenile production does not compensate for adult mortality). Sinks will ultimately go extinct unless they are "rescued" from extinction by receiving immigrants from another subpopulation (Brown and Kodric Brown 1977, Pulliam 1988). Thus, understanding source sink metapopulations requires knowledge of population demography at the subpopulation level, the habitat conditions responsible for variation in subpopulation demography, and the movement of individuals among source and sink habitat types.

In recent years, evidence has accumulated that the viability status of a subpopulation (source or sink) is strongly influenced by habitat size and shape (Harris 1984, Robinson 1992, Hoover et al. in press, Robinson et al. in prep, Donovan et al. manuscript). For some species, per capita reproduction is greatest in large, contiguous tracts of habitat, and reproduction declines as habitats are reduced in size (Faaborg et al. 1993). In such species, large tracts of habitat consist of source populations, while small, isolated habitats are dominated by sink populations (Robinson 1992, Donovan et al. manuscript). In this situation, the persistence of sinks in any metapopulation depends upon maintenance of large, intact source habitats (Pulliam 1988, Temple and Cary 1988, Howe et al. 1991).

Because source habitats are vital for metapopulation viability and longevity, and in light of increasing anthropogenic habitat alteration and fragmentation, it is important to understand how alteration of source habitats affects the size and structure of the overall metapopulation. Here, we develop a baseline source sink model in which reproduction is a function of habitat size, and then modify the baseline model to assess how fragmentation of source habitat affects different types of species. Although many source sink models have been developed in recent years (e.g., Pulliam 1988, Pulliam and Danielson 1991, Howe et al. 1991, Danielson 1992, Davis and Howe 1992), none have examined explicitly how metapopulations respond to incremental fragmentation of source habitat and how this response may vary depending upon the life history attributes of a species.

Our objectives were to: 1) develop a baseline source sink metapopulation model in which juveniles disperse uni-directionally from an area of high productivity (the source) to an area of low productivity (the sink), 2) modify the baseline model to examine how fragmentation of source habitat affects metapopulation size and structure for four hypothetical passerine species in which fragmentation differentially reduces reproduction, and 3) modify the baseline model so that juvenile dispersal between the source and the sink is bi directional, and examine how fragmentation of source habitat differentially affects metapopulation size and structure of six hypothetical passerine species with varying intrinsic dispersal regimes. We refer to these models as the baseline model, the fragmentation model, and the dispersal model, respectively.

We illustrate the properties of the models with a hypothetical migratory bird species whose reproductive success declines as habitats are fragmented. The reproductive traits of this hypothetical species, though, are derived from actual values measured for avian species in fragmented and unfragmented habitats in the Midwestern United States (Donovan et al., manuscript). Migratory birds are excellent organisms for examining source and sink metapopulation dynamics where reproduction (i.e., source sink status) is a function of habitat size (Temple and Cary 1988, Robinson 1992, Hoover et al. in press, Donovan et al. manuscript). In North America, many migratory bird populations are distributed in areas that are both favorable and unfavorable for reproduction, but because birds are highly vagile organisms, movement of individuals among source and sink habitats is likely (e.g., Stacey and Taper 1991, Robinson 1992). Fragmentation may limit the reproductive success of forest nesting migrants in several ways (Faaborg et al. 1993). As habitats become fragmented, birds experience increased nest predation (Hoover et al. in press, Paton 1994), increased brood parasitism by the Brown headed Cowbird (Molothrus ater, reviewed by Robinson et al. 1993), and decreased pairing success (Gibbs and Faaborg 1990, Villard et a1.1993). The result is that fewer young are produced in fragmented forests than contiguous forests. Thus, migratory passerines are well suited for investigating how metapopulations respond to incremental fragmentation of source habitat and how this response may vary depending upon the lire history attributes of a species.

MODEL DESCRIPTION

For all three models we view a species' global population as occupying two discrete types of habitat: 1) source habitat, where habitat conditions are favorable for reproduction, and 2) sink habitat, where habitat conditions are less favorable for reproduction (sensu Pulliam 1988). When individuals are censused, some fraction of the population is located within source habitat and some fraction is located within sink habitat. We assumed that source and sink habitat is uniformly distributed throughout the species' range.

In our model, a population of a migratory bird species occupies non breeding habitat in the winter, then migrates to North American breeding habitat in the spring in year (t) (Figure 1). At that time, juveniles born in year (t 1) disperse to their first breeding territory in either the source or the sink. In all three models, only juveniles disperse, and all dispersal occurs in the spring. Once territories are secured in the source and sink, birds reproduce at habitat specific rates, and populations are censused immediately after fledging. We simulated population growth for 200 years to ensure the population attained equilibrium, and discuss all results in terms of equilibrium population size, i.e., when the population is stable and not growing.

In the baseline model, we examine the number of individuals within four different classes at equilibrium: 1) adults m the source, 2) juveniles in the source, 3) adults in the sink, and 4) juveniles in the sink. We refer to the combined population of the four habitat/age classes as the metapopulation size, and the partitioning of individuals among the four habitat/age classes as the metapopulation structure. In the fragmentation and dispersal models, we relate the proportion of the adult population located within the source and the sink at equilibrium to source productivity and the amount of dispersal, respectively.

The Baseline Model

In the baseline model, juveniles disperse uni-directionally from an area of high productivity (the source) to an area of low productivity (the sink); this dispersal of juveniles from source to sink is dependent on source density. Adults do not disperse. Thus, the censused population size of each habitat/age class in a given year depends on three parameters: class fecundity, class survival rate, and how many juveniles dispersed and established their first breeding territory inside or outside of the class population.

In the baseline model, we assumed that all adults were habitat faithful, regardless of their nesting success in the previous year, (i.e., adults in the source in year t will return to the source in year (t + 1), and adults in the sink in year (t) will return to the sink in year (t +1). This assumption is supported because most dispersal in migratory passerines occurs as natal dispersal, or the movement of an individual from its birthplace to its first breeding territory (Greenwood and Harvey 1982). Once a breeding territory is secured, adults generally show strong philopatry to a generalized site (Martin and Li 1992).

Second, we assumed that all juveniles produced in the source seek their first breeding territory in the source, and that all juveniles produced in the sink seek their first breeding territory in the sink. Under the guise that 'sub optimal' habitat is plentiful, we assumed that all individuals seeking a territory in the sink acquired one. However, we assumed that successful acquisition of a territory in the source is density dependent, where the probability of acquiring a source territory decreases as the number of individuals seeking a source territory (including last year's adults) increases (Figure 2). This assumption is well supported because most forest nesting migrant passerines are territorial, and breeding population size is regulated by the number of territories a habitat possesses (Holmes and Sturges 1975). We used the following equation to describe density dependent dispersal from the source:

$$S = A^2 / (A^2 + X^2),$$

where S is the probability of successfully attaining a source territory, X is the total number of individuals seeking a source territory at the time of territory establishment in early spring, and A is a term that varies the success rate of territory acquisition by placing a "lid" on the number of individuals that occupy the source. When A = X, then 50% of the individuals that seek territories in the source will successfully attain one. The total number of individuals seeking a breeding territory in the source in year (t+l) consists of:

(# of adults in the source in year (t) * adult survivorship) + # of juvenile searchers(t+1)

In the baseline model, the number of juvenile searchers in year (t + 1) consists only of those juveniles produced in the source in year (t). We arbitrarily set A as 200 individuals in the source. If X is very large relative to A, the probability of successfully attaining a source territory is small. All individuals that are not successful in acquiring a source territory disperse to the sink. The effect of A on S and X is shown in Figure 2.

Third, we assumed that adult and juvenile survival rates were not habitat specific, i.e., the probability that a sink adult survived from year (t) to year (t+l) was the same as that of a source adult. This assumption is warranted because 1) most mortality pressures are constant throughout the year for birds (Ricklefs 1973), and since the breeding season represents approximately 1/4 of the annual cycle, most mortality in birds probably occurs during the non breeding season (Greenberg 1980), 2) breeding populations are interspersed during the non breeding season (Ramos and Warner 1980) and consequently individuals are equally exposed to mortality threats during that time, 3) preliminary comparisons of Ovenbird survival on fragments and contiguous forests in Missouri have shown no differences in adult survival rates between these two habitats (Porneluzi, pers. com.), and 4) there is no direct evidence that mortality on females during the breeding season is higher on fragmented habitats than contiguous habitats (Donovan et al., manuscript). We assumed the survival of juveniles and adults included any "cost" of searching for a breeding territory or dispersing from one habitat type to the other (but see Danielson 1991).

Given these basic model assumptions, we used the following difference equations to describe the population size of each class:

> <u>Source Adults</u>(t+l) _ (# source adults(t) * adult survival) + (# juveniles produced in the source(t) * juvenile survival) * probability of successfully attaining a source territory.
>
> <u>Sink Adults</u>(t+ 1) _ (# sink adults(t) * adult survival) + (#juveniles produced in the sink(t) * juvenile survival) + (# juveniles produced in the source (t) * juvenile survival) * (1 probability of successfully attaining a source territory).
>
> <u>Source Juveniles</u>(t+1) _ (# source adults(t+l) * source fecundity).
>
> <u>Sink Juveniles</u>(t+1) _ (# sink adults(t+1) * sink fecundity).

Fragmentation Model

Our objective in developing a fragmentation model was to assess how the metapopulation responds to incremental fragmentation of source habitat, and how this response may vary among species. We examined four types of hypothetical birds, one derived from observed field data, and three "modeled" species. These hypothetical species vary in their reproductive response to fragmentation of source habitats, e.g., reproductive success steeply declines as source habitat is fragmented in one of the hypothetical species, but only slightly declines in another. Although we refer to these species as hypothetical species, the four species reflect the range of observed variation in reproductive success of migrant passerines in source habitats. This variation occurs both within a species and among species. For example, we observed that in unfragmented habitats Ovenbird populations could function either as strong sources or weak sources. We also observed that within the same unfragmented habitat, some species produced more offspring per year than others (Donovan et al., manuscript). Thus, we used the four hypothetical species to assess the sensitivity of source fragmentation to changes in the reproductive strength of the source. As in the baseline model, all breeding individuals seek a territory in their natal habitat type first, but some disperse from source to sink because success in acquiring a source territory is density dependent.

We describe the fragmentation model below in terms of the hypothetical species whose reproductive attributes were derived from field observations, and later relate how we modified these attributes for the other three hypothetical species. We assumed that fecundity is a function of core habitat, defined as the percentage of habitat greater than 250 meters from a habitat edge (Figure 3). As habitats become more fragmented, core area is lost and a greater proportion of the habitat is subject to detrimental edge effects which, in turn, reduces nesting success (reviewed by Faaborg et al. 1993, Paten 1994). Thus, as core habitat decreases, fecundity decreases. This key assumption is strongly supported by field observations of migratory bird nesting success in forested habitats that vary in the amount of core habitat throughout the Midwest United States (Robinson et al. manuscript in prep, and see below). We described the relationship between core area and fecundity as:

$$\text{fecundity}(\%\ \text{core}) = \text{maximum observed fecundity}\ (c + \%\text{core}) / (b + c + \%\ \text{core}),$$

where fecundity (% core) is the mean number of female offspring per adult female per year in a source habitat with some percentage of core, maximum observed fecundity is the maximum number of female offspring per adult female per year based on field observations, and b and c were fitted constants. This equation produced a curve that has asymptotes at $x = (b+c)$ and $y =$ theoretical maximum fecundity, where theoretical maximum fecundity is the maximum number of female offspring produced per female per year (Figure 3).

To derive b and c in the equation above, we used two known points based on field observations of three forest nesting migrants from our fragmentation studies in Missouri and Wisconsin. These points were: (average percent core in the sink, average fecundity in the sink) and (0% core in sink, average fecundity at 0% core, Figure 3). The derived curve passes through these two points and also through a third point based on field observations: (average % core in the source, average fecundity in the source, Figure 3). For example, we observed that fecundity averaged 0.4 female offspring per female per year in landscapes with no core habitat, 0.62 female offspring in landscapes that averaged 6.21% core habitat, and 1.62 female offspring in landscapes that average 73.1% core habitat (Table 1).

In addition to reducing the fecundity of females, fragmentation of the source habitat also decreases the probability that an individual will successfully attain a territory in the source. In the fragmentation model, we considered success in attaining a source territory as a function of percent core, where A = % source core*200. Thus, fragmenting the core from 100% to 50% reduces A to 100 individuals, and the probability of successfully acquiring a source territory is decreased (Figure 2).

Because the fragmenting core habitat may affect fecundity differentially for various species (Robinson et al. manuscript), we examined three additional hypothetical species by varying the fecundity versus core curve previously described. By varying the point (average % core in the source, average fecundity in the source) among the three, additional hypothetical species, we were able to determine how fragmentation of source habitats might affect metapopulation size and structure differently for different types of species. Only the source fecundity varied in these curves, i.e., we kept fecundity at 0% core constant and average sink fecundity constant among curves, but changed the " reproductive strength" of the source among curves by changing the fecundity of the source from 1.4 to 2.0 to 2.4 female offspring per adult female per year (Figure 3). This relationship could be explored by varying sink reproduction as well. However, we chose to vary the reproductive strength of the source and kept the reproductive parameters of the sink constant because per capita reproduction is higher in the source, and the response of metapopulations to fragmentation of source habitats is probably most sensitive to changes in this parameter. In addition, the variation in the number of female offspring per female per year among the three species we studied was greater when some core habitat was present compared to the variation when no core was present (Table 1). Thus, there is biological support to varying reproduction in source habitats. Within each curve, we reduced the percent of core in the source, which in turn reduced source fecundity (Figure 3). We then compared how habitat fragmentation affects metapopulation size and structure for all four hypothetical species.

Dispersal Model

A second objective in developing a fragmentation model was to assess how fragmentation of source habitat affects metapopulation size and structure for six hypothetical species that vary in their intrinsic propensity to disperse. In source and sink metapopulations, the maintenance of sinks depends upon immigrants that dispersed from another subpopulation (Pulliam 1988). Yet, as source habitats are fragmented and source productivity is weakened, intrinsic dispersal may have negative connotations for the metapopulation at large (Davis and Howe 1992).

As previously mentioned, most dispersal in passerines occurs as a young bird moves from its birthplace to its first breeding territory. Intensive banding studies on passerines have shown, for example, that fewer than 1% of all banded nestlings subsequently return as breeding adults to a study area (Greenwood and Harvey 1982, Payne and Payne 1993, Holmes and Sherry 1992). Although these young birds do not exhibit site philopatry, it is not clear whether they exhibit some degree of habitat fidelity. For example, a nestling born in the heavily forested Missouri Ozarks may disperse to an Illinois forest, but whether it will preferentially establish its first breeding territory in a large forest or on a small fragment is not clear. Because this "natural propensity to disperse" or "innate dispersal" changes the proportion of the population occupying each habitat type, it may have profound effects on metapopulation size and structure.

In the baseline model, we described a situation where all juveniles return to their natal habitat type. In the dispersal model, we examined how fragmentation of source habitats affects the metapopulation size and structure in five hypothetical species whose juveniles vary in their natural propensity to disperse to a different habitat type. We defined "D" as the innate propensity of juveniles to disperse from their natal habitat type to the alternative habitat type. If the natural "dispersal" rate> D> is 0.25> then 25% of the individuals born in the source will seek to establish a breeding territory in the sink, and 25% of the individuals born in the sink will seek to establish a breeding territory in the source. The remaining 75% of individuals will seek a breeding territory in their natal habitat. Similarly, if D = 0.5, then the probability an individual will seek a territory in its natal habitat is 50%. The six hypothetical species have intrinsic dispersal rates of D = 0, 0.1, 0.2, 0.3, 0.4, and 0.5 respectively. For each species, we changed the "reproductive strength" of the source via habitat fragmentation and determined the size and proportion of the adult population in the source and the sink.

In the dispersal model, we modified the basic model difference equations to compute the population size of the adult classes. The juvenile equations are the same as the baseline model:

> <u>Source Adults</u>(t+l) (= # source adults(t) * adult survival) + ((#juveniles produced in the source(t) that did not disperse to the sink) + (# juveniles produced in the sink(t) that dispersed from sink to source)) * (juvenile survival) * (probability of successfully attaining a source territory).
>
> <u>Sink Adults</u>(t+1) _ (# sink adults(t) * adult survival) + ((# juveniles produced in the [sink(t) that did not disperse to the source) + (# juveniles produced in the source(t) .' that dispersed from source to sink)) * (juvenile survival) + (# juveniles seeking a territory in the source) * (1 probability of successfully attaining a source territory)* juvenile survival);
> where the # of juveniles seeking a territory in the source = (the # of juveniles produced in the source(t) that did not disperse to the sink + # of juveniles produced in the sink (t) that dispersed to the source).

MODEL PARAMETERIZATION

For the generalized migratory passerine species, we used the baseline estimates of 0.62 for adult survival and 0.31 for juvenile survival that were derived by Greenburg (1980) for passerines. These values have been used in modeling migrant bird populations in several studies (Temple and Cary 1988, Howe et al. 1991, Thompson 1993). In the baseline model only, we modified adult survival (0.52 and 0.72) to examine the sensitivity of that estimate on the metapopulation size and structure. This range in adult survival (0.52 0.72) encompasses most forest nesting migratory passeriformes (Martin and Li 1992, Nichols et al. 1981). In the fragmentation and dispersal models, we used 0.62 for adult survival to focus attention on the risks of habitat fragmentation and dispersal on metapopulation dynamics; changing adult survival in these models does not qualitatively affect the results.

We used reproductive data from our ongoing fragmentation studies in Missouri and Wisconsin, in which we surveyed birds and monitored reproductive success on fragmented and contiguous forest tracts in each state (see Donovan et al., in prep. for detailed site descriptions). We located and monitored Ovenbird (Seiurus aurocapillus), Red eyed Vireo (Vireo olivaceus),and Wood Thrush (Hylocichla mustelina) nests in fragmented and contiguous habitats in MO and WI from 1991 1994 (Table 1). Nests were located on 15 fragmented plots that averaged 6% core habitat and 14 unfragmented plots that averaged 73% core habitat. We monitored all nests until the fate of the nest was known, and recorded the number of young that successfully fledged a nest. To obtain reproductive estimates for a "generalized" forest nesting migrant, we pooled all nests over years to obtain the mean number of fledglings in both large, unfragmented forests and small, isolated fragments. In both MO and WI, reproductive success was significantly lower in fragmented than unfragmented habitats; the fragments consisted of population sinks while the unfragmented habitats consisted of population sources. We computed the mean number of female fledglings per adult female as the mean number of fledglings per study area divided by two (Table 1, see Donovan et al. (in prep) for more detailed information on productivity analyses). To estimate the fecundity of a generalized migrant at 0% core, we sub sampled our total nest sample bY randomly selecting 30 nests known to be located within 250m of a forest edge and calculated the average number of fledglings for nests located outside core forest habitat (Table 1).

For each of our study areas, we derived average forest cover landscape statistics from U.S. Geological Survey land use and land cover digital data (Office of Geographic and Cartographic Research, Reston, VA). For each plot (n =15 fragmented plots, n =14 contiguous plots), we determined the proportion of forest >_250 m from a non forest edge within 101m of the plot (Fragstats, Forest Science Dept., Oregon State University, Corvallis, OR). We refer to this proportion of non edge forest as core area. We averaged the proportion of core area for fragments (n =15) and contiguous areas (n =14) to define the fragmented and unfragmented habitats studied. Thus, we ascertained reproductive success in two landscapes: fragmented landscapes averaged 6% core habitat, while the contiguous landscapes averaged 73% core habitat (Table 1).

RESULTS

Baseline Model

In all baseline models, the metapopulation stabilized within 20 to 60 years. Metapopulation size and structure at equilibrium were sensitive to changes in adult survival (Figure 4). When baseline adult survival was 0.62 (Figure 4a), the majority of the censused population consisted of juveniles in the source, followed by source adults, sink adults, and sink juveniles. At equilibrium, approximately 78% of the juveniles from year (t 1) that sought a territory in the source population successfully attained a source territory, while the remainder failed to acquire a source territory and dispersed into the sink (Figure 4b). This relatively low level of dispersal from source to sink, combined with low reproduction in the sink and thus a small number of juveniles from year (t 1) seeking territories in the sink, stabilized the metapopulation such that most of the individuals occur in the source habitat.

This trend is even more apparent when adult survival was reduced to 0.52 (low adult survival, Figure 4c), such that most juveniles (>90%) produced in year (t 1) that sought a territory in the source were successful in attaining one (Figure 4d). Very few juveniles dispersed to the sink; the population size of sink individuals was maintained at low levels by paltry reproduction in the sink and the few source juveniles that dispersed to the sink. A second consequence of low adult survival was that the metapopulation size at equilibrium was substantially reduced.

By contrast, when adult survival was increased to 0.72, the majority of the censused population consisted of adults in the sink (high adult survival, Figure 4e). When the bulk of the adult population was located within the sink, then most juvenile production occurred in the sink, even though per capita productivity was relatively low. This occurred because we assumed that sink habitat was widely available and that population size in the sink was not limited. The remainder of the metapopulation at equilibrium consisted of source juveniles and source adults (Figure 4e). At equilibrium, the number of juveniles from year (t - 1) that sought a territory in the source population was high compared to the base adult survival and low adult survival, but only 5$% successfully attained a source territory; 42% dispersed into the sink (Figure 4f). This relatively high dispersal from source to sink maintained the metapopulation size at high levels and the bulk of the metapopulation occurred in the sink.

Fragmentation Model

Because we considered fecundity a function of percent core habitat (Robinson et al. manuscript), fragmentation of the source population reduced metapopulation size and affected metapopulation structure for all four hypothetical species. However, as fragmentation progressed, the proportion and number of adults in the source and sink at equilibrium varied among the 4 hypothetical species (Figure 5). For the hypothetical species whose source reproduction was low, any fragmentation of source habitat resulted in loss of sink populations because source productivity was not sufficient to rescue sinks from extinction (Figure 5a). For the three other hypothetical species, incremental fragmentation of the source resulted in a steady decline in source population, but the decline in the sink population varied dramatically (Figure 5).

For the hypothetical species with reproductive traits derived from observations (1.62 female offspring per adult female per year at 73% core habitat), fragmentation of the source reduced the equilibrium adult population size in both the source and the sink in a nearly Parallel fashion (Figure 5b). In this species, when the source core area was reduced to 25% core area, the metapopulation went extinct because the source is not able to sustain itself or provide immigrants to the sink habitat.

For the hypothetical species whose source fecundity was moderate (2.0 female offspring per adult female per year with 73% core habitat), most of the adult population resided in sink habitat (Figure 5c). This occurred. because increased source fecundity allowed migration of individuals from the source to the sink, maintaining the metapopulation at higher levels. Fragmentation of source core habitat, and concomitant decrease in fecundity of the source, resulted in decreased metapopulation size, but this decrease was more readily apparent in the sink than in the source (Figure 5c). When the source core habitat was reduced to 50%, the number of adults in the source and the sink was approximately equal. Further reduction in source core habitat resulted in a metapopulation where most adults occurred in the source and fewer occur in the sink.

For the hypothetical species whose source productivity was high (2 4 female offspring per adult female per year at 73% core habitat), the metapopulation size was large compared to the previous examples, and fragmentation of the source habitat from 100% core to 50% core resulted in a strong reduction of the sink population while the source equilibrium population declined only slightly by comparison (Figure 5d). When the source core habitat was reduced to 40%, the number of adults in the source and the sink was approximately equal; further fragmentation resulted in a metapopulation where most adults occur in the source.

Dispersal Model

The reduction in source fecundity via habitat fragmentation affected metapopulation size and structure differently for species that varied in their intrinsic rates of dispersal (Figure 6). For all 6 hypothetical species that varied in their intrinsic dispersal rates, the reduction in source fecundity via habitat fragmentation (high source fecundity to medium source fecundity to observed source fecundity to low source fecundity) resulted in overall metapopulation decline and ultimate extinction (Figure. 6). However, species with high rates of intrinsic dispersal declined more quickly than species with low intrinsic dispersal (Figure 6). For example, in an unfragmented situation where source fecundity was high, the metapopulation size and structure of the hypothetical species with low intrinsic dispersal (D =1) consisted of approximately 45 adult females in the source and 100 adult females in the sink (Figure 6a). As source fecundity was reduced via habitat fragmentation, the sink population was reduced to 60 adult females (Figure 6b), and further reduction in source productivity via habitat fragmentation reduced the sink population to approximately 25 adult females (Figure 6c). Further fragmentation resulted in a very small metapopulation that consisted of individuals located in the source (Figure 6d).

By contrast, species with a high intrinsic rata of dispersal was more quickly affected by fragmentation of source habitats. For example, in an unfragmented situation where source fecundity was high, a species with high intrinsic dispersal (D = 0.4) maintained the same metapopulation size and structure as a species with low intrinsic dispersal (Figure 6a). As with the less dispersing species, a reduction in source fecundity (from high to medium) resulted in reduced metapopulation size, primarily in the number of individuals that occurred in the sink (Figure 6b). However, further reduction in source fecundity via habitat fragmentation (from medium to observed) resulted in near extinction of the metapopulation. This occurred because too many individuals strayed away from favorable habitat to poor habitat, and an overall metapopulation declined.

DISCUSSION

Our models showed that metapopulations will decline in response to incremental fragmentation of source habitat, but the manner of decline varied depending upon the life history attributes of a species. Fragmentation resulted in rapid metapopulation extinction for species with "weak" reproduction in the source, i.e., populations that do not produce a w large excess of individuals. For species that produced a large excess of individuals in the source, initial population declines occurred in sink habitats. These results have important connotations for migratory bird populations.

The widespread decline of some migratory species has been attributed to habitat fragmentation (Temple and Cary 1988, Askins et al. 1990, Faaborg et al. 1993). These studies corroborate that migrant bird population declines are most apparent in small, fragmented habitats, while populations in large, unfragmented habitats are not declining (Askins et al. 1990). Field observations show that small, isolated fragments are dominated by population sinks (Robinson 1992 Donovan et al. manuscript). Without immigration, migratory bird populations are expected to decline in small habitats. We suggest, however, that fragmentation of source habitats may result in population declines in the sink by decreasing the number of potential immigrants available to rescue sinks from extinction. These declines may occur without concomitant population declines in the source. Thus, the reduction in density of some bird species on small habitats (so called area sensitive species) may be the result of two non exclusive processes: 1) poor reproductive success in small habitats when immigration is negligible (reviewed in Faaborg et al. 1993, Donovan et al. in prep), or 2) fragmentation of source habitat, which affects that number of immigrants available to "rescue" populations on fragments from extinction. Based on these results, we re emphasize the need to identify and protect large, intact source habitats throughout a species' breeding range to ensure long term metapopulation survival.

Our fragmentation model was qualitatively different than the fragmentation model developed by Temple and Cary (1988) in several ways. First, we presented a range of hypothetical species and modeled how incremental fragmentation differentially affected species depending on their life history traits, while Temple and Cary (1988) demonstrated how the metapopulation of a single migratory bird will respond to three fragmentation scenarios. In this sense, we presented a larger picture that enables a more clear interpretation of their results. Second, Temple and Cary (1988) assumed that fecundity is a function of distance to edge, while we assumed that fecundity was a function of habitat core area within 10 km of a particular habitat (Robinson et al. in prep). Although edge effects do exist for many species, we believe that reproductive success of migratory birds is governed by overall landscape quality and pattern. For example, Wood Thrushes (Hylocichla mustelina) nesting in relatively large forest blocks (>1000 ha) but in a highly fragmented landscape in southern Illinois experience the same reduced reproductive success as thrushes nesting on much smaller forests in the same landscape (Robinson, pers. comet.), i.e., edge effects extend well beyond 200 m. In this situation, features of the surrounding landscape may be more important in determining reproductive success than distance from edge per se. For such species, examination of core habitat within a given area should more realistically predict population changes with fragmentation (Robinson et al., manuscript).

It has been appreciated. for many years that habitat fragmentation is detrimental for species with limited dispersal capacity (Gilpin 1987). In these species, decreased habitat and population size can erode the genetic variability and increase the probability of local extinction (Gilpin 1987). Until recently, habitat fragmentation has not been a major concern in highly vagile species because movement of individuals among sources and sinks can preserve the genetic diversity of the population and "rescue" subpopulations from local extinction (Brown and Kodric Brown 1977). Such "rescue" however, may be at a cost to the larger, global population. Recently developed mathematical models predict that demographic systems driven by frequent extinction and recolonization of subpopulations result in rapid reduction in effective population size and loss of global genetic variation for the species as a whole, even in otherwise abundant species (McCauley 1993). In this scenario, interacting sources and sinks may actually lose genetic variation faster than a panmictic population with the same number of individuals.

In addition to a genetic cost of rescue, our results suggest there may be a demographic "cost" to rescuing sinks from extinction if individuals disperse from areas that are favorable for reproduction to less favorable areas. This "cost" is most pronounced when fragmentation diminishes the ability of the source to produce a large excess of individuals. When reproduction in the source is diminished, metapopulation size declines for species with high intrinsic rates of dispersal because individuals tend to stray away from high quality habitats (sources) to low quality habitats; sinks function to "drain" the source population and result in population decline in both the source and the sink. By contrast, species with low intrinsic dispersal are comparatively less affected by habitat fragmentation because individuals tend to return to habitats where per capita reproduction is the highest in the source. Our results support the hypothesis put forth bY Howe et al. (1991) and Davis and Howe (1992), that species with high intrinsic dispersal should be most affected by habitat degradation.

Although the relevant demographic unit for maintaining migratory bird populations is the metapopulation (Villard et al. 1992), traditional management practices and the majority of Neotropical migrant bird studies continue to focus on local scale (or subpopulation) demography. We believe conservation strategies must acknowledge metapopulation structure and protect regionally important source areas. Future research should encompass a broader landscape perspective, and might include, for example, identification of the geographic scale by which populations are connected by dispersal, identification of the intrinsic and extrinsic factors that govern dispersal among sources and sinks, and how these vary among species. Verification of our model predictions is needed to lend credence to the metapopulation dynamics proposed in our models. Studies of the details of metapopulation dynamics of widespread species are needed to provide critical information necessary for directing long term conservation efforts.

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LITERATURE CITED

Askins, R. A., J. F. Lynch, and R. Greenberg. 1990. Population declines in migratory birds in eastern North America. Curr. Ornith. 7:1 57.

Brown, J. H., and A. Kodric Brown. 1977. Turnover rates in insular biogeography: effect of immigration and extinction. Ecology 58:445 449.

Danielson, B. J. 1992. Habitat selection, interspecific interactions and landscape composition. Evol. Ecol. 6:399 411.

Davis, G. J., and R. W. Howe. 1992. Juvenile dispersal, limited breeding sites, and the dynamics of metapopulations. Theor. Pop. Biol. 41:184 207.

Faaborg, J., M. C. Brittingham, T. M. Donovan, and J. Blake. 1993. Habitat fragmentation in the temperate zone: a perspective for managers. Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO USA.

Gibbs, J. P., and J. Faaborg. 1990. Estimating the viability of Ovenbird and Kentucky warbler populations in forest fragments. Conserv. Biol. 4:193 196.

Greenberg, R. 1980. Demographic aspects of long distance migration. Pages 493 504 in Migrant birds in the Neotropics: Ecology, behavior, distribution, and conservation (A. Keast and E. S. Morton, eds.). Smithsonian Institution Press, Washington, D.C.

Gilpin, M. E. 1987. Spatial structure and population viability. Pages 125 139 in Viable populations for conservation (M. E. Soule, ed.). Cambridge University Press, Cambridge.

Greenwood, P. J., and P. H. Harvey. 1982. The natal and breeding dispersal of birds. Ann. Rev. Ecol. Syst. 13:1 21.

Hagan, J. M., and D. W. Johnston. 1992. Ecology and conservation of Neotropical migrant landbirds. Smithsonian Institution Press, Washington, D.C.

Hanski, L, and M. Gilpin. 1991. Metapopulation dynamics: Brief history and conceptual domain. Biol. J. Linnean Soc. 42:3 16.

Harris, L.D. 1984. The fragmented forest: Island biogeographic theory and preservation of biotic diversity. Univ. Chicago Press, Chicago, Illinois.

Holmes, R. T., and F. W. Sturges. 1975. Bird community dynamics and energetics in anorthern hardwoods ecosystem. J. Anim. Ecol. 44:175 200.

Holmes, R. T., and T. W. Sherry. 1992. Site fidelity of migratory warblers in temperate breeding and Neotropical wintering areas: Implications for population dynamics, habitat selection, and conservation. ,fin Ecology and conservation of Neotropical migrant landbirds (J. M. Hagan III and D. W. Johnston, eds.). Smithsonian Institution Press, Washington D.C.

Hoover, J. P., M. C. Brittingham, and L. J. Goodrich. In press. Nesting success of Wood. Thrushes in a fragmented forest landscape in Pennsylvania. Auk.

Howe, R. W., G. J. Davis, and V. Mosca. 1991. The demographic significance of 'sink' populations. Biol. Conserv. 57:239 255.

Levins, R. 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. Bull. Entomol. Soc. Amer. 15:237 240.

Levins, R. 1970. Extinction. Pages 77 107 in Some mathematical problems in biology. (M. Gerstenhaber, ed.). American Mathematical Society, Providence, Rhode Island.

Martin, T. E., and P. Li. 1992. Life history traits of open versus cavity nesting birds. Ecology 73:579 592.

McCauley, D. 1993. Genetic consequences of extinction and recolonization in fragmented habitats. Pages 217 233 in Biotic interactions and global change (P. Kareiva, J. Kingsolver, and R. Huey, eds.). Sinauer Associates, Inc., Sunderland, MA.

Nichols, J. D., B. R. Noon, S. L. Stokes, and J. E. Nines. 1981. Remarks on the use of mark recapture methodology in estimating avian population size. Studies in Avian Biology 6:121 136.

Paton, P. W. 1994. The effect of edge on avian nest success: How strong is the evidence? Conserv. Biol. 8:17 26.

Payne, R. B., and L. L. Payne. 1993. Breeding dispersal in Indigo buntings: circumstance and consequences for breeding success arid population structure. Condor 95:1 24.

Pulliam, H. R. 1988. Sources, sinks, and population regulation. Am. Nat. 132:652 661.

Pulliam, H. R., and B. J. Danielson. 1991. Sources, sinks, and habitat selection: a landscape perspective on population dynamics. Am. Nat. 137:S50 S66.

Ramos, M. A., and D. W. Warner. 1980. Analysis of North American subspecies of migrant birds wintering in Los Tuxtlas, southern Veracruz, Mexico. Pages 173 Migrant birds in the Neotropics: Ecology, behavior, distribution, and conservation (A. Keast and E. S. Morton, eds.). Smithsonian Institution Press, Washington, D.C.

Ricklefs, R. L. 1973. Fecundity, mortality, and avian demography. Pages 366-435 in Breeding biology of birds (D.S. Farner, ed.). National Academy of Science.

Robinson, S. K. 1992. Population dynamics of breeding Neotropical migrants in a fragmented Illinois landscape. Pages 408 418 ii Ecology and conservation of Neotropical migrant landbirds (J. M. Hagan III and D. W. Johnston, eds.). Smithsonian Institution Press, Washington and London.

Robinson, S. K., J. A. Grzybowski, S. I. Rothstein, M. C. Brittingham, L. J. Petit, and F. R. Thompson. 1993. Management implications of Cowbird parasitism for neotropical migrant songbirds. h Status and management of Neotropical migratory birds (D. Finch and P. Stengel, eds.). USDA Forest Service Rocky Mountain Forest and Range Experiment Station. Fort Collins, Colorado.

Stacey, P. B. and M. Taper. 1992. Environmental variation and the persistence of small populations. Ecol. Applic. 2:18 29.

Temple, S. A., and J. R. Cary. 1988. Modeling dynamics of habitat interior bird populations in fragmented landscapes. Conserv. Biol. 2:340 347.

Thompson, F. R. III. 1993. Simulated responses of a forest interior bird population to forest management options in central hardwood forests of the United States. Conserv. Biol. 7:325 333.

Villard, M. A., K. Freemark, and G. Merriam. 1992. Metapopulation theory and Neotropical migrant birds in temperate forests: an emperical investigation. In Ecology and conservation of Neotropical migrant landbirds (J. M. Hagan and D. W. Johnston, eds.). Smithsonian Institution Press, Washington D.C.

Villard, M. A., P. R. Martin, and C. G. Drummond. 1993. Habitat fragmentation and pairing success in the Ovenbird (Seiurus aurocapillus). Auk 110:759 768.

Figure 1. Life cycle of hypothetical species used in all models. In all models, an annual census is taken immediately after the breeding season in both source and sink habitats. Adult and juvenile individuals survive the non breeding season with a probability (PA) and (PA and seek breeding territories in the following breeding season. Dispersal occurs prior to breeding, and individuals reproduce according to habitat specific reproduction rates.

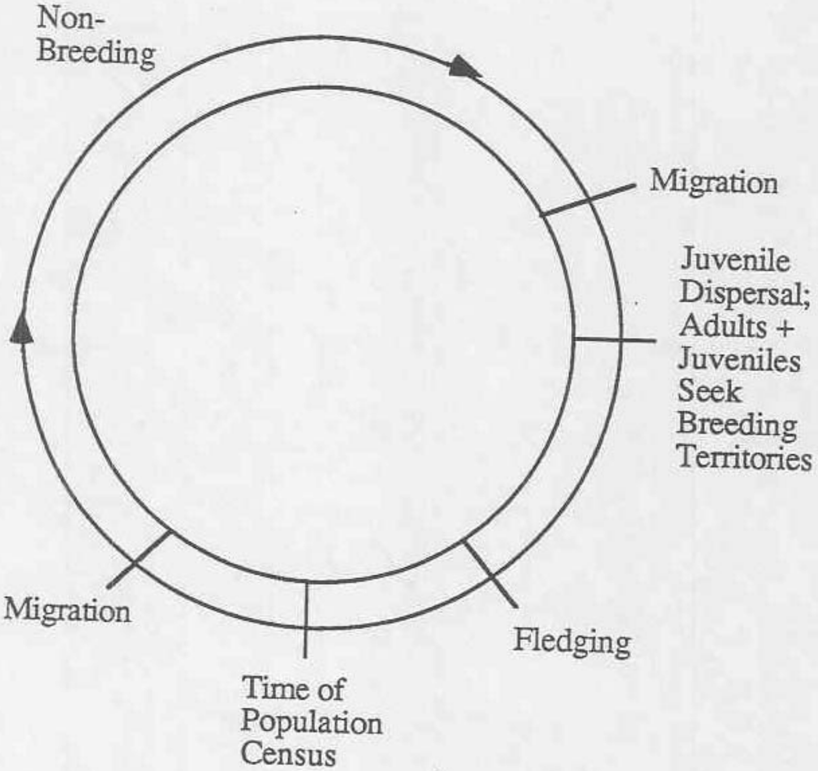
Non-
Breeding
Migration
Juvenile
Dispersal;
Adults +
Juveniles
Seek
Breeding
Territories
Fledging
Time of
Population
Census
Migration

Figure 2. Relationship between the total number of individuals seeking a territory in the source just prior to breeding and the probability of successfully attaining a source territory. Three conditions of "A" are depicted, where A represents the number of individuals that can hold territories in the source habitat

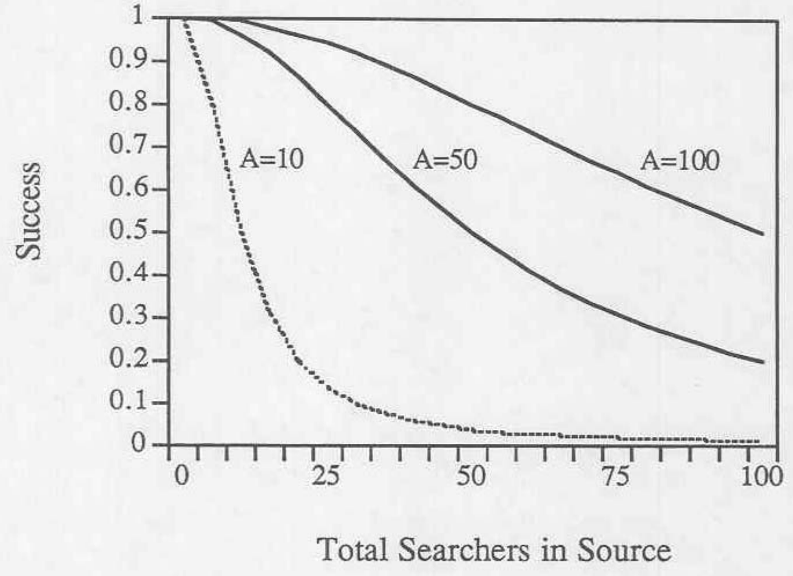
Success
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
A=10
A=50
A=100
0
25
50
75
100
Total Searchers in Source

Figure 3. Relationship between fecundity and. percent core habitat for four hypothetical species. The solid curve represents a hypothetical species whose reproductive traits were observed in the field: three fitted points depict observed values from our field studies in fragmented and unfragmented habitats in Wisconsin and Missouri. The dashed curves show the relationship between fecundity and core for three additional hypothetical species.

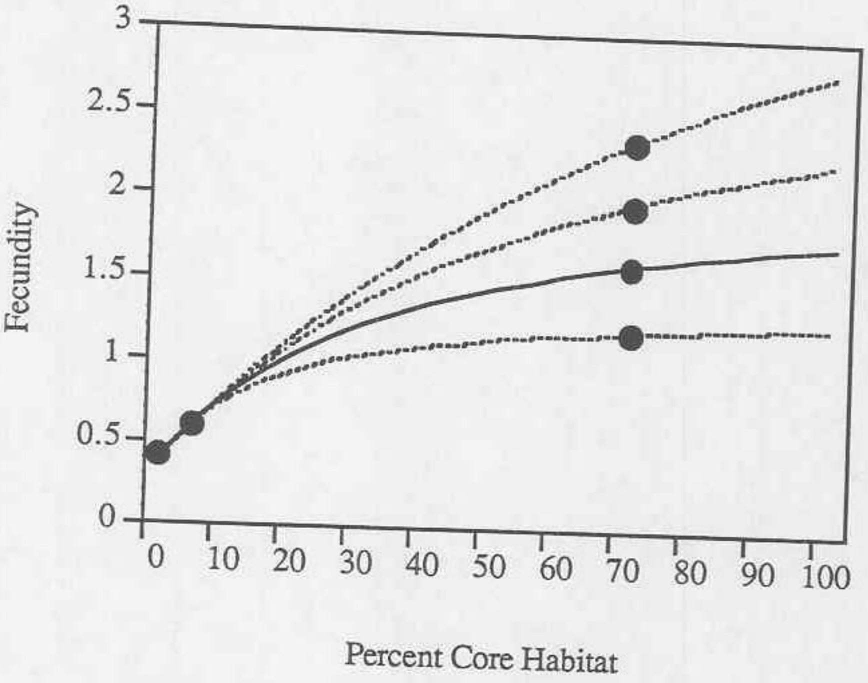
3
2.5
2
1.5
1
0.5
0
Fecundity
0
10
20
30
40
50
60
70
80
90
100
Percent Core Habitat

Figure 4. Results of baseline model simulations of a generalized forest nesting migratory bird in which there is density dependent dispersal from source to sink. Panels a, c, and e depict metapopulation size and structure after 200 generations. Panels b, d, and f illustrate density dependent dispersal as a function of the number of juveniles from the previous year that seek territories in the source habitat. Baseline adult survival = 0.62 (a and b); low adult survival = 0.52 (c and d); high adult survival = 0.72 (e and f).

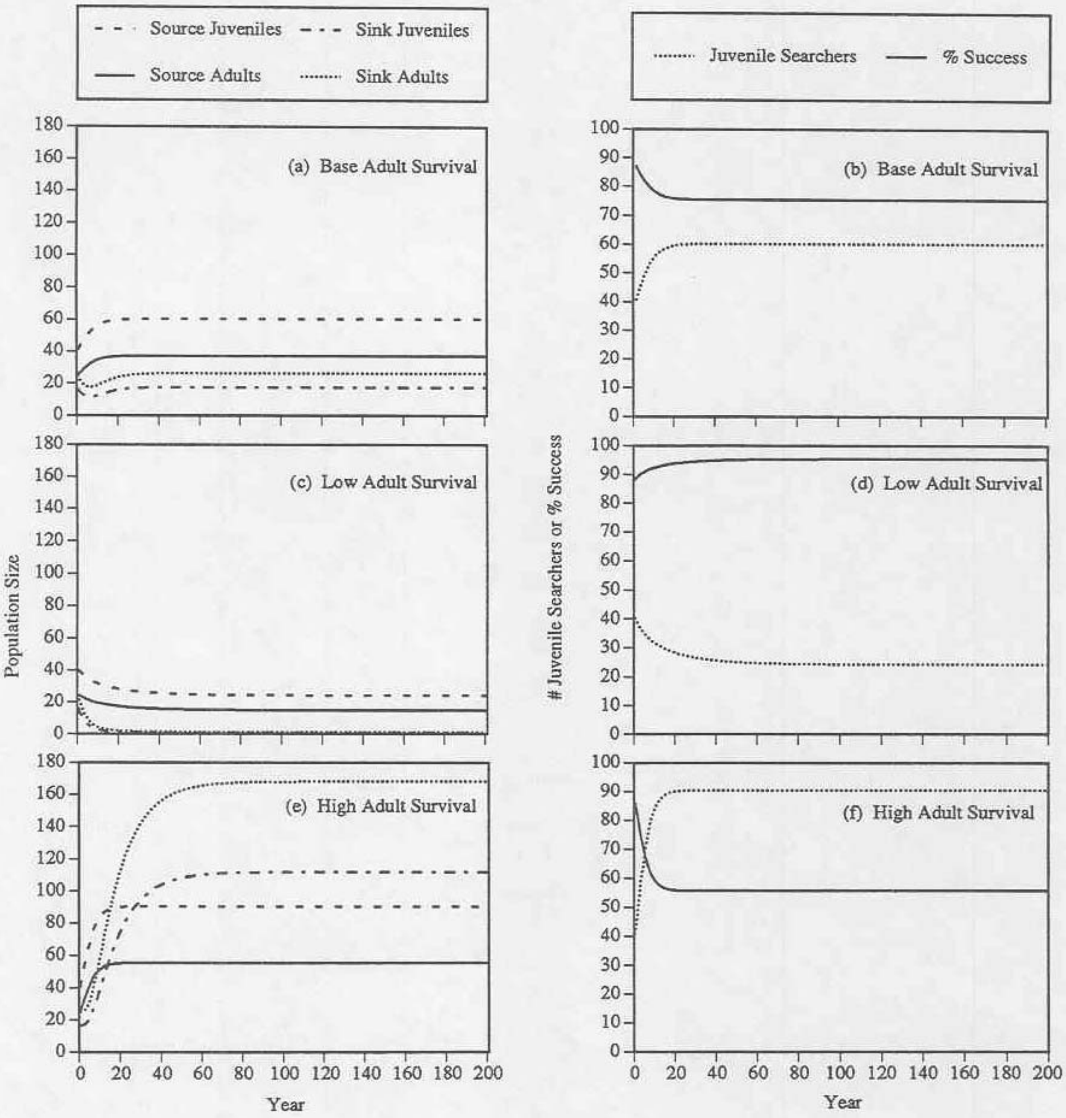
Source Juveniles
Sink Juveniles
Source Adults
Sink Adults
Juvenile Searchers
% Success
(a) Base Adult Survival
(b) Base Adult Survival
(c) Low Adult Survival
(d) Low Adult Survival
(e) High Adult Survival
(f) High Adult Survival
Population Size
Juvenile Searchers or % Success
0
20
40
60
80
100
120
140
160
180
0
10
20
30
40
50
60
70
80
90
100
0 20 40 60 80 100 120 140 160 180 200
Year
0 20 40 60 80 100 120 140 160 180 200
Year

Figure 5. Relationship between equilibrium population size of adults in the source (solid curve) and the sink (dashed curve) and percent core habitat in the source for four hypothetical species whose reproductive response to habitat fragmentation varies.

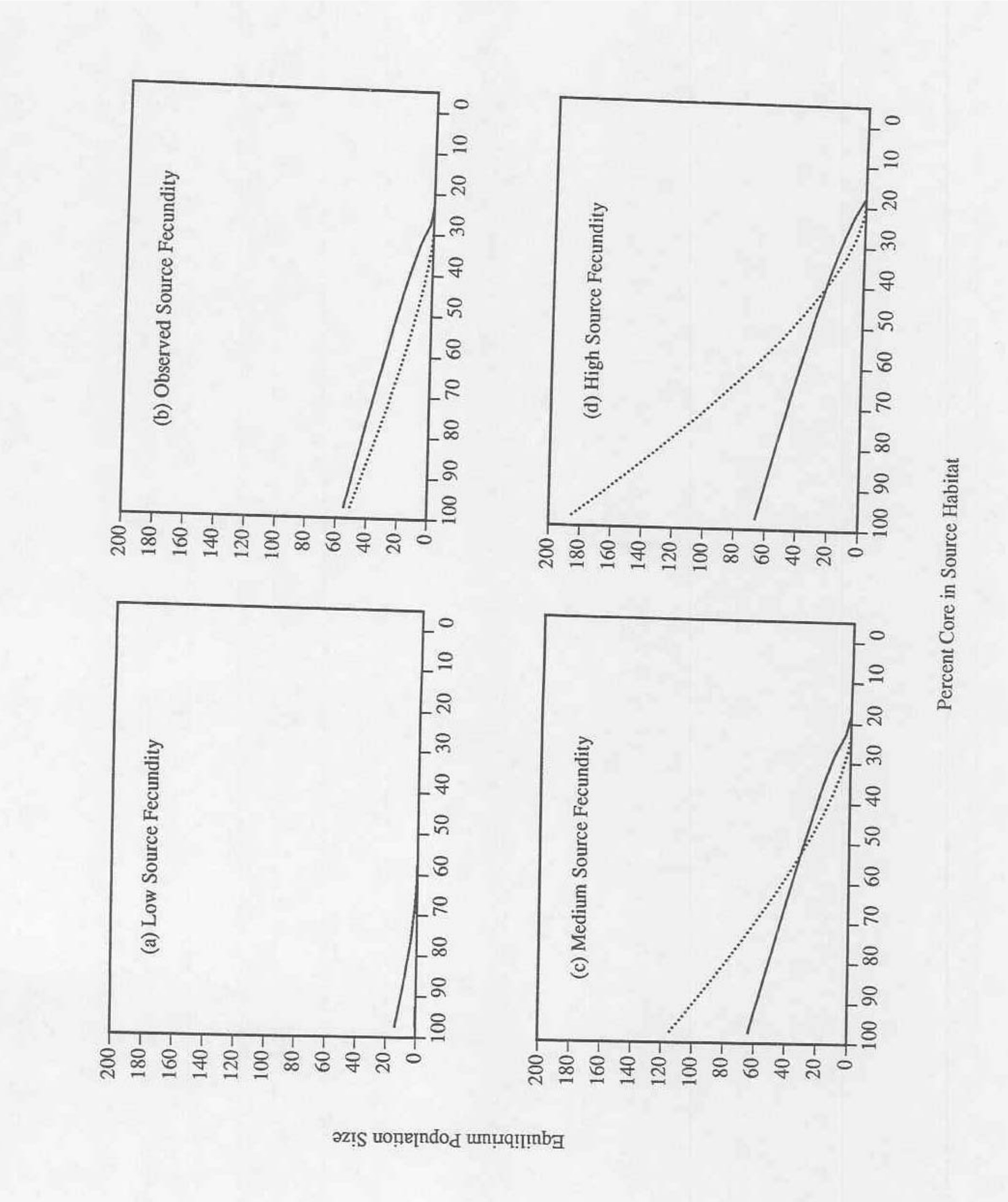
(a) Low Source Fecundity
(b) Observed Source Fecundity
(c) Medium Source Fecundity
(d) High Source Fecundity
Equilibrium Population Size
Percent Core in Source Habitat
200
180
160
140
120
100
80
60
40
20
0
100
90
80
70
60
50
40
30
20
10
0

Figure 6. Relationship between equilibrium population size of adults in source (solid curve) and sink (dashed curve) habitats for six hypothetical species that vary in their intrinsic dispersal rate. Dispersal rate (D) is on the X axis, and ranges from 0 to 0.5 for the six species. Source fecundity is reduced from high source fecundity (a) to medium source fecundity (b) to observed source fecundity (c) to low source fecundity (d) via habitat fragmentation.

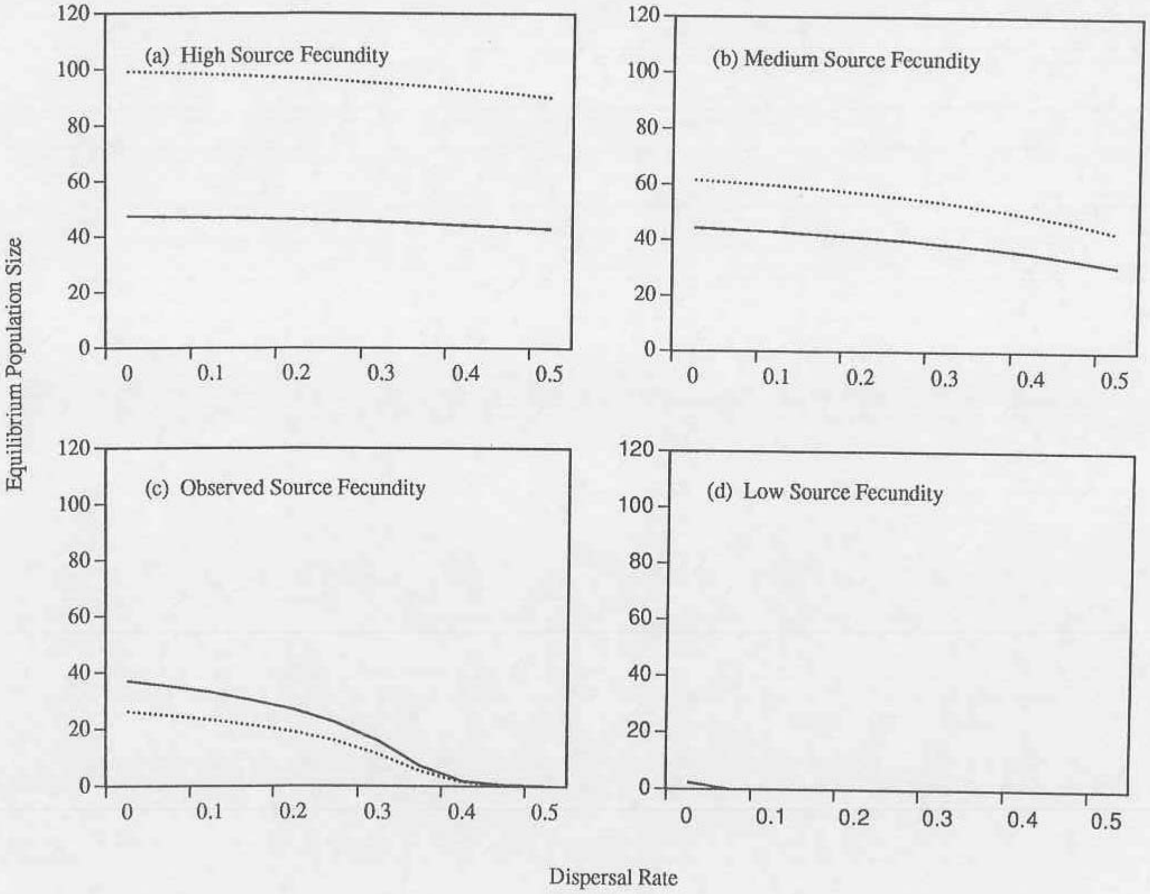
Equilibrium Population Size
(a) High Source Fecundity
(b) Medium Source Fecundity
(c) Observed Source Fecundity
(d) Low Source Fecundity
120
100
80
60
40
20
0
0
0.1
0.2
0.3
0.4
0.5
Dispersal Rate

Table 1. Demographic parameters used in baseline and fragmentation models for a generalized forest-nesting migratory bird.

Landscape	% Core Habitat	Fecundity (S.D)	Nest Sample Size	Adult Survival	Juvenile Survival	Starting Adult Population Size
Unfragmented	73.12	(low).......1.20	203	(base) 0.62	0.31	25 females
		(observed).1.62 (.30)		(low) 0.52	0.31	25 females
		(med)...... 2.00		(high) 0.72	0.31	25 females
		(high)......2.40				
Fragmented	6.21	(observed).0.66 (.43)	124	(base) 0.62	0.31	25 females
0% Core	0.00	(observed).0.40 (.17)	30			

VITA

Therese Donovan was born and raised in the Chicago area. She obtained a B.S. in Biology, a teaching certificate in Botany, and an M.S. in Environmental Biology from Eastern Illinois University. She worked as a high school biology teacher and badminton coach in the Chicago area and as a naturalist and volunteer coordinator for the Lake County Forest Preserve District. She received a Ph.D. in Biology from the University of Missouri Columbia in 1994. She has recently obtained a Postdoctoral position as an ecologist for the North Central Experiment Station, USDA Forest Service, in Columbia, Missouri.